Population Ecology of North Atlantic Humpback Whales

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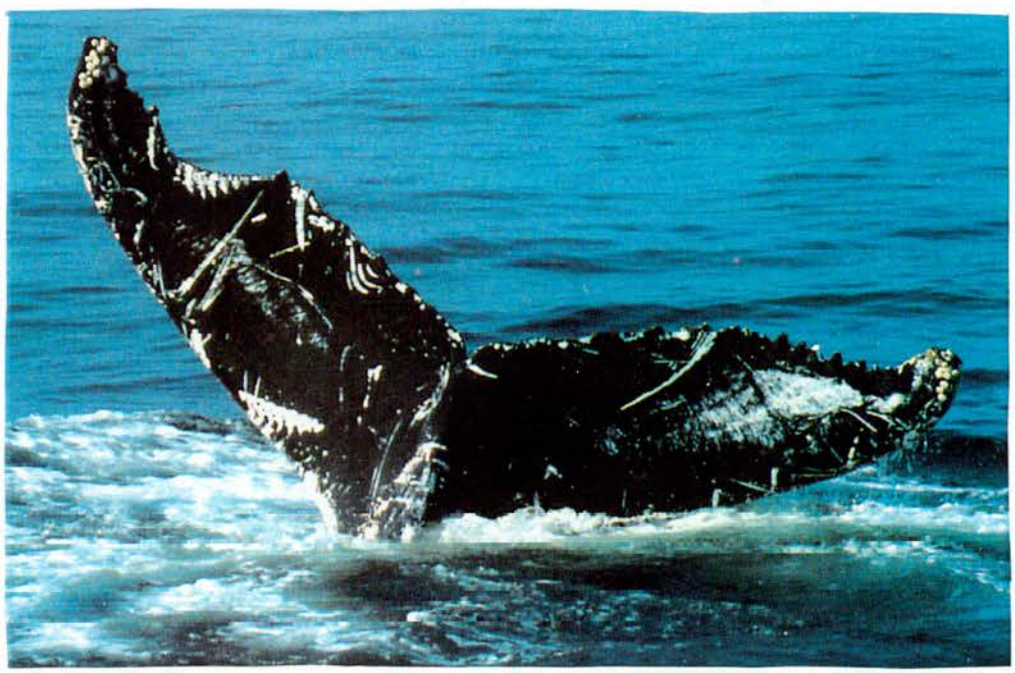

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North Atlantic Humpback Whales

Peter T. Stevick

Submitted in partial fulfilment of the requirements for the degree of Ph.D.

University of St Andrews

April 4, 2001

I, Peter T. Stevick, hereby certify that this thesis, which is approximately 43,000 words in length, as been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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Abstract

This study investigated the population ecology of North Atlantic humpback whales on an ocean-basin-wide scale. Individual animals were identified by natural markings between 1978 and 1993 and also by genetic markers in 1992 and 1993. The abundance for 1992-1993 is estimated by capture-recapture methods as 11,570 (95% CI 10,290-13,390). The trend in abundance estimates from 1979-1993 indicates an annual rate of increase of 0.0420 (SE 0.0044, r^2 0.83). All abundance estimates utilise methodological improvements over previous estimates including a correction to account for errors in identification. This correction is developed using results from a large-scale double-marking experiment using genetic tags and natural markings for identification. The correction is stratified by photographic quality.

The ocean-basin-wide nature of this study, the use of cluster analysis to delineate feeding aggregations, the use of transit distances to examine movement across a range of scales and knowledge of the sex of a large portion of the sample, provide new insights into population spatial structuring. Movement patterns on the feeding grounds demonstrate high levels of fidelity to quite small regions; the median between year re-sighting distance is <40 km. Re-sighting patterns differ between areas and over time. Some of these differences are related to prey distribution. Animals from all feeding areas are sighted on a common breeding ground, and occur there at similar rates, though the timing of their sightings on the breeding grounds is related to their feeding ground origin.

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Preface

While North Atlantic humpback whales are the most intensively studied group of large whales in the world, a considerable amount remains unknown regarding their population ecology and the status of this population remains difficult to assess. In spite of being abundant and apparently increasing in several regions of the North Atlantic Ocean, humpback whales remain listed as endangered under the United States Endangered Species Act and as vulnerable by the World Conservation Union (IUCN). Published estimates of abundance have increased over the past 30 years. However, comparison of these estimates is complicated by methodological differences between studies and the poor precision of some estimates.

These difficulties are compounded by uncertainties about the structure of the population. Two stocks have been proposed within the North Atlantic, one associated with the western and the other with the eastern margin of the ocean basin. Most information to date has been derived from animals in the west; data relevant to the eastern stock have been limited and difficult to interpret. Further, geographically discrete feeding aggregations have been described within the North Atlantic which are not related to breeding populations, and a low rate of exchange has been documented between them.

In this thesis, I address questions of population structuring and trends in abundance in the North Atlantic Ocean. Much of what has been learned about humpback whales in recent decades has derived from studies of naturally marked individuals. I use the database of sighting records maintained by the North Atlantic Humpback Whale Catalogue (NAHWC) and the collection from the

Years of the North Atlantic Humpback Whale (YoNAH) project. Between them they represent approximately 18,850 sightings of humpback whales from much of the known humpback whale habitat in the North Atlantic spanning the period from 1978-1993.

The thesis is primarily structured as a series of papers. As these were prepared individually for publication, some overlap is inevitable. In order to minimise repetition, however, I initially present two chapters containing information of general relevance to the subsequent material. The first chapter *Biogeography of humpback whales* introduces the distribution, movement patterns, history of exploitation and evidence for current abundance and recovery. Chapter two, *Identification methods and databases*, presents information on identification by natural and genetic markings, the field methodologies used, the two primary projects and associated databases on which these analyses are based. For the sake of clarity, some of the information from these chapters is summarised in subsequent chapters.

The next two chapters cover estimation of abundance and trends in abundance. Errors are known to occur in identification of individuals by natural markings, and these errors are related to photographic quality. One method for minimising the bias caused by these errors is to restrict the sample to only photographs of the highest quality. This reduces sample size, however, decreasing precision. The first chapter in this section, *Errors in identification using natural markings: rates, sources and effects of errors on capture-recapture estimates of abundance*, presents the results of a double marking experiment through which I determine photo-quality specific error rates, and develop and apply a correction to account for these errors. In the next chapter, *Trends in abundance of North*

Atlantic humpback whales, I utilise 14 years of capture-recapture results to calculate abundance estimates and the resulting trend in abundance.

The following three chapters address issues of population structure. The first, *Population spatial structuring on the feeding grounds*, examines site fidelity to specific locations on the feeding grounds and the pattern of spatial structuring which results from this, along with an examination of some of the factors which may influence the observed patterns. Chapter six, *Migration timing is related to feeding ground origin in the North Atlantic humpback whale: panmixis reconsidered?*, presents information on individuals sighted on both the feeding and breeding ranges, the re-sighting rates from the different feeding grounds and differences in migration timing between individuals from different feeding grounds and between males and females. These two chapters raise issues regarding the status of individuals from Norway for which the analysis is limited by the small sample from that area. Thus the final chapter, *Migratory destinations of humpback whales from Norwegian and adjacent waters: evidence for stock identity*, presents the results of the only comparison completed to date between the YoNAH and NAHWC collections. Photographs collected by the Norwegian YoNAH field project were compared to both collections in order to address the role of the West Indies as a migratory destination for humpback whales from Norway.

Publications arising from this thesis with notes on authorship

Listed below are a number of publications related to this thesis. Five chapters are presented in the form of papers in the thesis. An additional

publication represents material included in the introduction. One paper has been published, one is in press and another is in review. The remaining three are being reviewed by co-authors in preparation for submission.

As this thesis utilises data from two large-scale, international collaborative projects, all of the publications arising from it are, appropriately, multi-authored papers. I have contributed substantially to all phases of both projects. I was a major contributor to and photo analyst for the NAHWC for many years. I managed photographic analysis for the project from 1991 until 1998, overseeing or conducting all photographic comparison and maintaining the database. I am one of the principal investigators of the YoNAH project. I conducted and supervised YoNAH field sampling in Newfoundland and was a primary photographer in the West Indies. I personally photographed at least 450 individual whales during the two years of YoNAH. I supervised all photographic comparison and quality coding for the project, developed and maintained the project database and managed the budget.

Three of these papers (4, 5 & 6) contain primary findings from the YoNAH project, and thus all of the principals from that project are included in authorship, at least a dozen authors on each. Though this list varies slightly from paper to paper, these individuals are responsible for conceiving of and developing the YoNAH project, supervising data collection in the field and/or overseeing laboratory analyses. My first authorship on these papers and inclusion of the papers in this thesis is a reflection of my primary role in analysis and writing. All of the analyses for these papers were developed and conducted by me, and the writing is mine. Phil Hammond's position as last author reflects his supervisory

role. Contributions of the other authors specific to the analyses included in the thesis are noted in the acknowledgements for each related chapter.

Paper 3 presents the results of a double-marking experiment. The second set of marking results was provided through the genetics laboratory work of Per Palsbøll and his collaborators. Phil Hammond and Tim Smith helped me to develop the material along the way and kept me on the mathematical straight and narrow. Phil helped me to try and estimate variance using a bootstrap procedure. When we admitted defeat, Mark Bravington stepped in. The estimation of variance for abundance estimates presented in paper 3 is decidedly Mark's work, not mine. His procedure is included as Appendix B in this thesis to outline the technique I applied. While all of these people played important roles, the body of the paper reflects my ideas, analyses and writing.

Paper 1 presents the result of photographic comparison between Norwegian waters and the West Indies. My co-authors were responsible for collecting these data, while Nils additionally provided funding for the much of the photographic analysis. However, I conducted the photo comparison, analysed the results and wrote the paper.

Publication 2 was prepared as a textbook chapter reviewing the literature on movement patterns of all marine mammals. It contains material prepared initially for the introduction to this thesis, while other material that I prepared for the chapter has been incorporated into other parts of the thesis. My specific review of baleen whale movements was modified for more general application and taxonomically expanded with the help of co-authors Bernie McConnell and Phil Hammond. I co-ordinated the writing, organisation and logistics. The sections that

are included in this thesis remain wholly my work, though I wish to thank Bernie and Phil for expanding my taxonomic horizons.

Publications

1) Stevick, P. T., Øien, N. & Mattila, D. K. 1999. Migratory destinations of humpback whales from Norwegian and adjacent waters: evidence for stock identity. *Journal of Cetacean Research and Management* 1: 147-152.

2) Stevick, P.T, B. J. McConnell and P. S. Hammond. In press. Patterns of movement. *In* A.R.Hoelzel (*ed.*) Marine Mammal Biology: An Evolutionary Approach. Blackwell Books.

3) Stevick, P. T., T. D. Smith, M. V. Bravington, P. J. Palsbøll and P. S. Hammond. In press. Errors in identification of individuals by natural markings: rates, sources and effects on capture-recapture estimates of abundance. *Canadian Journal of Fisheries and Aquatic Sciences*.

4) Stevick, P. T., D. K. Mattila, J. Robbins, J. Allen, P. J. Clapham, S. K. Katona, F. Larsen, J. Lien, P. J. Palsbøll, J. Sigurjónsson, T. D. Smith, N. Øien and P. S. Hammond. In review. Migration timing is related to high latitude origin in North Atlantic humpback whales: panmixis reconsidered? *Proceedings of the Royal Society, Series B.*

5) Stevick, P. T., J. Allen, P. J. Clapham, S. K. Katona, F. Larsen, J. Lien, D. K. Mattila, P. J. Palsbøll, R. Sears, J. Sigurjónsson, T. D. Smith, G. Vikingsson, N. Øien and P. S. Hammond. In prep. Population spatial structure of North Atlantic humpback whales investigated by movements of identified individuals.

6) Stevick, P. T., J. Allen, P. J. Clapham, N Friday, S. K. Katona, F. Larsen, J. Lien, D. K. Mattila, P. J. Palsbøll, J. Sigurjónsson, T. D. Smith, N. Øien and P. S. Hammond. In prep. Trends in abundance of North Atlantic humpback whales, 1979-1993.

Acknowledgements

This thesis is the culmination of work that has engaged me for many years, and the number of people to whom I owe a large measure of gratitude is enormous. Without them, I would never have made it to this point.

First and foremost, of course, is my family who provided endless help and encouragement. Nancy has provided me with incalculable love and support over the years. She gave up a great deal to pack up house and move here, and I am most grateful to her for everything she contributed to making this degree a reality. Heather and Andy provided a reliable excuse to wrestle, look for badgers, play football or search for fossils with a clear conscious. My parents were enormously supportive of this effort, as they have been of all my endeavours. My sister Carol provided a number of much-needed visits and regular helpings of moral support. And special thanks to my grandmother for remaining an ardent fan.

The results presented here are the product of an unprecedented collaborative effort and would not have been possible without the dedication and hard work of many individuals. In particular, I would like to thank the principal investigators of the YoNAH project. The original conspirators include Judy Allen, Phil Clapham, Phil Hammond, Steve Katona, Finn Larsen, Jon Lien, Dave Mattila, Per Palsbøll, Johann Sigurjónsson, Tim Smith and Nils Øien. This diverse group not only had the audacity to dream up this scheme, but also the persistence to carry it to fruition. In addition there are others who, like me, arrived at various later stages, Nancy Friday, Jooke Robbins and Gisli Vikingsson. I spent many enjoyable hours in the field with many of these people and many less enjoyable hours in meetings with most of them.

The field work was conducted by a skilled, enthusiastic and hardworking crew of many dozens of individuals from countries around the North Atlantic and beyond. Fernanda Marques was the ideal companion for an arduous journey up the east coast of Newfoundland in a small, overcrowded and usually leaking inflatable. She coped ably and with abundant good spirit with the difficulties which inevitably accompany such work. Rosie Seton helped me to learn the ins and outs of working in Newfoundland, where it seemed she knew everyone. Dwayne Pittman, Wayne Barney and Wayne Ledwell provided the logistical common sense and inventive repairs that kept the rest of us working. Among the many able crew in Newfoundland I wish to particularly thank Colin MacLeod, Megan McOsker, Dawn Nelson, Joanne Papineau, Missy Power, Christoph Richter, Sean Todd, Valeria Vergara and Lutz Werner. In Samana Bay and on Navidad Bank I was fortunate enough to work with Phil Clapham, who may never forgive me for finding the sperm whales on a day he had to return to port, Bob Bowman, the best captain I have had the pleasure to work with, Oswaldo Vasques who when not being a thorn in my side was great fun and a mean shot with a crossbow, and also Lydia Barnes, Tom Fernald, Finn Larsen, Hector Ramirez, Ditte Rendtorff and the indominable Jennifer Shuemaker.

Jon and Judy Lien opened their home to me and to my family. They provided good food (if not always for the faint hearted), better company, and I am forever grateful to them for introducing my children to the joys of keeping chickens. Jon's boundless energy, extensive knowledge and limitless imagination were an inspiration to me during my time in Newfoundland.

The NAHWC owes its existence to the continuing efforts of Steve Katona, Judy Allen and the hundreds of contributors who made it possible. I would

particularly like to thank Steve for getting it all started and for all of his support and encouragement over the years. The analysis of photographs is a time consuming, eye straining and often mind numbingly tedious task. YoNAH photographic analysis was cheerfully undertaken by Marti Crone, Tom Fernald, Shawn Hayward, Stephanie Martin, David Morin, Jen Rock, Rosie Seton, Nancy Stevick, Kate VanDine and Fred Wenzel with logistical support from numerous students from College of the Atlantic. Coding of photographs for image quality was conducted by Ozlem Uz and Tom Fernald with logistical help from Rosie Seton and Nancy Friday.

I could not have asked for a better supervisor than Phil Hammond. I have been quite spoilt by my time at the Gatty. Phil was willing to take a gamble on an old timer like me as a student, and in spite of all of his other commitments, his door really was always open. The SMRU staff were all knowledgeable, helpful and fun to be around. The other students were a tremendous resource, and many of the students and staff provided vital opportunities for me to get into the field occasionally.

Adjusting to life in a foreign county was made easier by a wonderful group of neighbours, particularly Winnie Armit, Denys Robey, and Andrew, Aileen, and Gordon Kennedy. Allan and Lyndesay Brown introduced me to catching swans from a kayak.

Financial support for the analyses reported here was provided in large measure by contracts from the United States Government, National Marine Fisheries Service, Northeast Fisheries Science Center. Tim Smith, as contracting officer, provided sound criticism of the work in progress and was always supportive. My tuition and other costs associated with being a student were

provided by the generosity of Mrs. B. H. Anderson. My sincere thanks to her, the Northern Trust Bank and the administrators of the Wm. Anderson Trust for all of their help. And, of course, thanks to Nancy for taking on a large share of the responsibility for earning our family a living these past three years.

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As an undergraduate, I had the very good fortune to know and study under Bill Drury. He helped me to develop an appreciation for the role of natural selection, an eye for details and a taste for the joy of studying nature. Ideas that he first exposed me to permeate this thesis. I wish that I were able to share it with him.

Finally, I would like to thank the whales who put up with me over the years. In spite of everything that could and usually did go wrong in the field, they always made it worth while being there. And just when I thought I had them figured out, they would go and surprise me. I hope they keep it up.

Chapter 1: Biogeography of humpback whales

Humpback whales (*Megaptera novaeangliae*) are cosmopolitan in distribution; they are found in every major ocean basin ranging from equatorial to polar waters. Because they are found near coastlines in many parts of their range and thus are relatively accessible to study, much is known about their population ecology. A great deal remains unknown, however, about their movement and distribution patterns and their abundance and conservation status.

Distribution and movement patterns

The distribution of organisms is a function of the resources they require. In a theoretical environment in which resources were abundant, uniformly distributed and stable, individuals would be widely distributed, and there would be little incentive to move. Resources are limited, however, and are clumped rather than distributed randomly or systematically in many, if not all, natural environments (Wiens 1997). Further, this environmental variability is a function of scale, both temporal and spatial (Kotliar & Wiens 1990). Patches of good or poor habitat for a given activity may extend over large areas and last for months or years, or they may be highly localised and change daily or weekly.

Another important feature of the environment influencing patterns of movement is its relative predictability. Environmental variability is itself dynamic; patches of good or poor habitat change over time and space. While increased productivity in the oceans is predictably associated with continental shelf breaks, the location of increased productivity in the open oceans associated

with meso-scale features (e.g. frontal systems) is often unpredictable and has to be actively sought. Prey resources that are abundant in an area for several consecutive years may suddenly collapse. Movement can thus be viewed as an adaptation to a patchy, unpredictable environment over a range of temporal and spatial scales.

Humpback whales have, therefore, evolved patterns of movement to help them to cope with and exploit the dynamic, variable and often unpredictable marine environment. These movements range from large-scale migrations between widely separated breeding areas and feeding areas, through to small-scale response to changes in prey availability whilst foraging.

Distribution

Humpback whales occur in all oceans (Clapham & Mead 1999). They are not known to occur in the Sea of Okhotsk (Clapham & Mead 1999) while data supporting the presence of humpback whales in the Bay of Bengal, Indonesia and the South China Sea region are equivocal (Reeves et al. 1991). Sightings in the Mediterranean Sea and the Gulf of Mexico are uncommon (Aguilar 1989; Weller et al. 1996).

Humpback whales are principally distributed over continental shelves or in coastal waters. In the Antarctic, however, they show no preference for any water depth or slope (Kasamatsu et al. 2000) and major concentrations occur in waters over 3,000m in depth (locations from Kasamatsu et al. 1996; Mackintosh 1965; Nicol et al. 2000; depth contours from Commonwealth of Australia map NPM/85/109.2). Recent acoustic monitoring detected high levels of humpback

whale song throughout the winter in pelagic waters off shore from their principal breeding ground (Clark 1995). Water depths in this region may exceed 8,000m.

Seasonal habitats

Humpback whales inhabit two distinct seasonal habitats. During the summer they are principally found in high latitude feeding grounds, while in winter they migrate to low latitude breeding grounds for calving and mating.

Foraging movements

Obtaining an adequate supply food is one of the most basic determinants of the survival and success of an individual. Mysticete cetaceans spend several months each year without access to food (see below). Most animals that undergo such protracted fasts enter a state of dormancy, diapause or hibernation to conserve energy (Begon et al. 1996). Humpback whales, to the contrary, are active and undertake extensive migratory movements during this fast. Thus they must obtain enough food during the productive summer months to survive, migrate and reproduce during their winter fast. Their distribution and foraging movements on the feeding grounds, then, are determined by the spatial and temporal distribution of food and its predictability.

Humpback whales prey on a wide range of items. In the Southern Hemisphere they feed largely on euphausiids (principally *Euphausia superba*) as do most Antarctic predators, but they also take other invertebrates and fish, at least in some areas (Nemoto 1959). In the Northern Hemisphere they take euphausiids, notably *Meganyctiphanes* and *Thysanoessa*, but feed extensively on schooling fishes including herring, capelin, mackerel, sardines, anchovies, sand

lance and pollock (Christensen et al. 1992a; Clapham et al. 1997; Clapham & Mead 1999; Mikhalev 1997; Mitchell 1973; Nemoto 1959; Tomilin 1957).

Such prey items are often associated with physical forms such as banks, canyons or the edge of the continental shelf, perhaps because oceanographic processes such as upwelling are associated with these features and lead to locally high productivity. The locations in which fish gather to spawn are also often associated with physical features. Such prey concentrations lead to associations between marine mammals and these features as well (Campagna et al. 2000; Hooker et al. 1999; Kenney & Winn 1986).

Prey may also be associated with transient oceanographic features such as meso-scale frontal systems. In spite of the very different foraging habits of the two species, both sperm whales and right whales have been shown to be associated with the boundaries of warm core rings (Biggs et al. 2000; Griffin 1999; Mate et al. 1997). The cold water entrainment along the edge of these rings is associated with higher levels of productivity than surrounding regions. Similarly, larger scale oceanographic features may concentrate prey. A strong relationship has been demonstrated between the density of both krill and their predators (including humpback whales) and oceanographic processes associated with the southern boundary of the Antarctic Circumpolar current (Nicol et al. 2000).

While foraging, the movements of marine mammals are determined by the size and density of prey patches, and the area over which patches may be predictably located (Jaquet & Whitehead 1999; Mayo & Marx 1990; Whitehead 1996). When in patches of high prey density, animals move so as to increase

their chances of staying within the patch. They turn more frequently and at greater angles. Upon leaving a high-density patch they move so as to maximise their chances of encountering another patch. This may entail travelling in a relatively straight path or a broad curve. Figure 1.1 illustrates the movements of right and sperm whales during foraging. Note the similarity in patterns of movement and the relationship between movement and foraging success, even at enormously different temporal and spatial scales. This 'area restricted search' behaviour in response to a patchy food resource is one of the primary mechanisms leading to aggregation of individuals (Begon et al. 1996).

Since some physical features may predictably lead to concentrations of prey, return to specific sites where prey has been abundant in the past may be a useful foraging strategy. The spatial scale of the predictability will determine the scale on which philopatry is demonstrated. Given the patchy distribution of prey, and area restricted search behaviour by whales, such philopatry to feeding sites will result in discontinuous distribution patterns.

Studies of philopatry have concentrated on the return of individuals to breeding sites (Anderson et al. 1992; Greenwood 1980; Lindberg et al. 1998; Pomeroy et al. 1994; Weatherhead & Forbes 1993). The ecological and evolutionary importance of fidelity to non-breeding areas is increasingly being recognised, however (Reed et al. 1998b; Robertson & Cooke 1999). High levels of fidelity have been documented to winter foraging areas and migratory staging areas in several groups of migratory birds (Cuadrado et al. 1995; McClelland et al. 1994; Rappole 1995; Reed et al. 1998b; Robertson & Cooke 1999). Similarly, seasonal movements of mammals often involve return to specific individual

ranges during times of year not associated with birth or mating (Boyce 1991; Nelson 1995; Schaefer & Luttich 1998; Thouless 1995).

Individuals that return to an area will have greater familiarity with the resources found there. This will allow them to exploit those resources and, in territorial species, to defend them more effectively. Rappole (1995 and references therein) showed that migrant thrushes that returned to wintering sites were more successful at obtaining feeding territories, obtained higher quality territories, and suffered less predation than did those which moved between years.

Feeding area philopatry is probably widespread in marine mammals. Studies of individually identified cetaceans consistently show high annual return rates to seasonal high-use areas (Agler et al. 1990; Calambokidis et al. 1996; Clapham et al. 1993a; Dorsey et al. 1990; Sears et al. 1990), though the scale at which the return is documented differs considerably between studies complicating comparison between them (see Koenig et al. 1996; Robertson & Cooke 1999).

However, a resource that is predictable for one or two seasons, or longer, may not always be so; in response, areas of high marine mammal density may shift in an unpredictable manner. Changes in the distribution of humpback, fin, right and sei whales off the northeastern US coast were associated with relative abundance of copepods, herring and sand eels (Payne et al. 1986; 1990; Weinrich et al. 1997), while areas utilised by harbor seals in the Moray Firth, Scotland were related to changes in the relative abundance of sandeels and sprats (Tollit et al. 1997). Exceptional oceanographic conditions in the Barents Sea caused the

capelin stock to collapse in 1986 (Christensen et al. 1992b). With no alternative prey available, starving harp seals then moved south down the coast of Norway (Nilssen et al. 1998), while humpback whales virtually disappeared from the Barents Sea east of 20° E between 1986 and 1989 (Christensen et al. 1992b).

In humpback whales, feeding ground fidelity is well documented. Feeding ground distribution is discontinuous, leading to geographically discrete groups of animals. In several areas high rates of return have been documented to these areas, and little movement has been observed between them (Baker et al. 1986; Calambokidis et al. 1996; Clapham et al. 1993a; Katona & Beard 1990; Katona & Beard 1991; Larsen & Hammond 2000; Paquet et al. 1997; Perry et al. 1990; Waite et al. 1999; Whitehead et al. 1982). Katona and Beard (1990) referred to these groups as feeding aggregations, while Baker et al. (1986) referred to them as sub-stocks.

There is not a one to one correspondence between feeding areas and breeding areas. In the North Atlantic, individuals from all feeding areas have been identified in the West Indies breeding ground (Chapter 6). In the North Pacific, on the other hand, individuals from the feeding ground in British Columbia, for example, have been identified in breeding grounds which span nearly 120° of longitude. They have been sighted near Ogasawara, Japan, in the Hawaiian Islands and from three sites near Mexico, the mainland coast, Baja California and the Revillagigedo islands (Darling et al. 1996; Darling & McSweeney 1985; Urbán R et al. 2000).

A possible exception to the pattern of animals from numerous feeding aggregations using common breeding grounds may exist in Costa Rica, where to

date only animals from the feeding ground off California have been identified, however this association is not reciprocal, with individuals from California also wintering in Mexico and Hawaii (Calambokidis et al. 2000).

Because of the breeding system of humpback whales (see Clapham 1996), young animals accompany their mother to her traditional feeding areas during their first year as dependent calves, but are not likely to travel to the feeding area associated with their father (Clapham et al. 1993b). This leads to site fidelity transmitted along maternal lines (Clapham & Mayo 1990; Katona & Beard 1990). There is evidence that this behaviour is maintained over many generations, as it is reflected in maternally inherited mitochondrial genetic markers, but not in nuclear markers (Larsen et al. 1996; Palsbøll et al. 1995). Such maternally directed spatial structuring is not unique to cetaceans. Similarity in seasonal habitat use and migration patterns have been observed to persist through multiple generations in white tailed deer, for example, and to be associated with maternal lines (Nelson 1998; Nelson & Mech 1999).

Feeding ground distribution

Humpback whale feeding grounds are located in productive temperate to polar waters (Katona 1986; Mackintosh 1965; Tomilin 1957).

In the North Atlantic, feeding grounds range between approximate latitudes 40° N off the U.S coast, and 78° N near Spizbergen. Distribution is largely over the continental shelf and in nearshore waters. Major concentrations are found in the Gulf of Maine and Georges Bank off the US coast, the south and east coasts of Newfoundland and Labrador, the Grand Banks, and in the Gulf of St Lawrence off eastern Canada, along the west Greenland coast south of 66° N,

in the Denmark Strait and off the south and east coasts of Iceland, near Jan Mayen and in the Barents Sea north of Norway (Christensen et al. 1992b; Clapham et al. 1993a; Hay 1982; Jonsgård 1966; Katona & Beard 1991; Kenney & Winn 1986; Larsen & Hammond 2000; Sigurjónsson & Gunnlaugsson 1990a; Smith et al. 1999; Whitehead 1982; Whitehead & Glass 1985; Whitehead et al. 1982).

In the North Pacific, feeding grounds occur along the coasts of California, Oregon and Washington as far south as 32° N (Calambokidis et al. 2000). They are also found in British Columbia, Southeast Alaska, the Gulf of Alaska and through the Alutian Islands extending at least to 60° N (Baker et al. 1985; 1986; Calambokidis et al. 1996; 2000; Darling & McSweeney 1985; Nishiwaki 1966; Perry et al. 1990; Tomilin 1957; Waite et al. 1999). There are limited data from catches to suggest that humpbacks formerly frequented waters further north in the western Bering Sea, perhaps as far north as 70° N (Nishiwaki 1966; Tomilin 1957).

In the Southern Hemisphere, five primary areas of concentration have been identified based upon distribution of catches (Mackintosh 1942), and six management areas have been defined (Donovan 1991). Five of these six areas coincide with high sighting densities from sighting surveys in the area; the exception being in Area II (Kasamatsu et al. 1996). The discreteness of these groupings is largely supported by 'Discovery' tag returns (Chittleborough 1965; Dawbin 1964; Dawbin 1966). In contrast to the Northern Hemisphere, productivity in the Antarctic is not associated with shallow waters and coastal margins, but more directly with frontal and current systems (Hindell et al. 1991;

Nicol et al. 2000; Tynan 1998). The region of greatest productivity in the Antarctic is located south of the Antarctic Convergence, which occurs between 55° and 65° S and thus highest whale density is found in this region (Mackintosh 1942). The Area II humpback group near South Georgia Island extends north to nearly 50° S and the Area V group in the Ross Sea extends south of 70° S (Kasamatsu et al. 1996; Mackintosh 1965).

Breeding movements

The resource requirements for giving birth and for mating are not necessarily the same as those for feeding, so the habitat used by animals for these activities are often different from those used at other times of year. In some marine species, for example, birth must take place on land.

During winter months, humpback whales are found in low latitude breeding grounds. It is in this region that calves are born and that mating is presumed to take place. In tropical regions, suitable prey for humpback whales is rarely available, and feeding is uncommon (Baraff et al. 1991). Thus, the distribution of whales on the breeding grounds is independent of food availability. The primary resource influencing distribution on the breeding grounds is the presence of conspecifics. The breeding system does not involve geographically exclusive territoriality and has been likened to a lek (Clapham 1996). Thus large aggregations of humpback whales in small areas are the norm during the breeding season, and most populations appear to have one or a small number of areas of concentration rather than numerous areas containing smaller groupings.

It is not known what factors influence habitat choice on the breeding grounds. Most known breeding areas are in shallow water over shoals or banks, with few whales seen in adjacent deep water habitats, suggesting that shallow water is an important habitat requirement, and deep water areas are relatively unimportant (Gannier 2000; Herman & Antinoja 1977; Mate et al. 1998; Swartz et al. 2000; Whitehead & Moore 1982; Winn et al. 1975), though the degree to which singing, an activity associated with breeding, has been recorded in deep waters may require re-examination of this assumption (Clark 1995). Some degree of segregation of mothers with newborns, particularly in sheltered areas near reefs or islands has been shown (Craig & Herman 2000; Flórez-González 1991; Smultea 1994; Whitehead & Moore 1982). It has also been proposed that mothers with calves are more common in peripheral areas (Mattila & Clapham 1989).

Because breeding grounds occur in tropical or sub-tropical regions, warm conditions would appear to be an important habitat requirement, though it is unclear why this might be (see critique by Corkeron & Connor 1999). It has been suggested that calving may occur in high latitudes which would be at odds with this theory. Ingebrigtsen (1929) reported on females pregnant with large foetuses taken off the Finmark coast in winter, though he did not report any newborn calves being present. Williamson (1961) reported a sighting of a calf off Canada in winter, though the timing of this sighting does not preclude the birth occurring in the tropics.

Because each population will utilise one or a small number of breeding sites, fidelity to breeding areas is certain to be high at broad geographical scales.

High rates of return to breeding areas have been documented in several regions (Chaloupka et al. 1999; Flórez-González 1991; Jenner & Jenner 1994; Katona & Beard 1991; Mattila et al. 1989; Perry et al. 1990; Urbán R et al. 1999). Limited movement between breeding areas has been observed (Chittleborough 1965; Darling & Cerchio 1993; Perry et al. 1990; Salden et al. 1999; Urbán R et al. 2000). While sample sizes are too small to evaluate quantitatively, three individuals observed to move between breeding sites are suspected to be males on the basis of reproductive behaviour, while none are identified as females (Darling & Cerchio 1993; Salden et al. 1999). This could indicate male biased dispersal, typical of mammalian reproductive systems (Greenwood 1980; Liberg & von Schantz 1985).

Evidence for fidelity on a smaller scale within overall breeding areas is more limited. Considerable movement within breeding grounds has been shown. The peak in abundance has been observed to shift within a breeding area through the season suggesting widespread, perhaps progressive movement (Baker & Herman 1981; Mattila & Clapham 1989; Whitehead & Moore 1982), and individual animals have been identified in multiple concentrations throughout a breeding area (Mattila et al. 1989; Mattila et al. 1994). Further, use of particular habitats by females appears to be linked to reproductive status, and thus will change from year to year (Craig & Herman 2000). On the other hand rates of return to specific banks or islands have been shown to be higher than rates of re-sighting to other locations both in the West Indies and in Hawaii (Cerchio et al. 1998; Katona & Beard 1990).

Breeding ground distribution

Many breeding areas occur at about 20° latitude, though they range from nearly 30° to the equator.

In the North Atlantic the principal breeding area occupies the Atlantic margin of the West Indies chain. The majority of the population occurs on Silver and Navidad Banks north of the Dominican Republic (Mattila et al. 1989; Whitehead & Moore 1982; Winn et al. 1975). Lesser concentrations occur off the northeast coast of the Dominican Republic, the west coast of Puerto Rico, Virgin and Anguilla Banks, throughout the eastern Caribbean islands as far as Trinidad, and also along the South American coast to the leeward Dutch Antilles (Debrot et al. 1998; Mattila & Clapham 1989; Mattila et al. 1994; Swartz et al. 2000). Resighting patterns suggest that these locations constitute a single breeding area (Mattila & Clapham 1989; Mattila et al. 1994; Stevick et al. 1999a). Some humpback whales are also seen in winter in the Cape Verde Islands, though the relationship between these individuals and those wintering elsewhere is not clear (Hazevoet & Wenzel 2000; Reiner et al. 1996).

In the North Pacific humpback whale breeding grounds occur off Okinawa and Ogasawara (Darling & Mori 1993; Nishiwaki 1959; Nishiwaki 1960), around the Hawaiian Islands (Herman & Antinoja 1977; Mobley et al. 1999), off Mexico (Urbán R & Aguayo L 1987) and Costa Rica (Calambokidis et al. 2000). Within Mexican waters, there appear to be two groups of animals with separate movement patterns and migratory destinations, one off mainland Mexico and Baja California, and the other off the Revillagigedo Islands (Urbán R et al. 2000). There is evidence for some limited movement between breeding

areas in the North Pacific (Perry et al. 1990; Salden et al. 1999; Urbán R et al. 2000).

In the Southern Hemisphere humpback whale breeding grounds occur along both margins of South America, extending along the coasts of Ecuador and Colombia, possibly as far as Costa Rica on the west coast (Acevado & Smultea 1995; Flórez-González 1991; Ben Haas pers. comm). This group extends well north of the equator and geographical, though not temporal overlap with animals from the Northern Hemisphere has been suggested (Acevado & Smultea 1995). On the east coast, the principal concentration occurs at Abrolhos Bank off the Brazilian coast (Salvatore Siciliano pers. comm.). Along the western coast of Africa, concentrations occur at the equator off the coast of Gabon (Dawbin 1997; Walsh et al. 2000). In the southwest Indian Ocean, breeding grounds are thought to occur along the coast of South Africa and Mozambique, the Comores Islands and the coast of Madagascar, though the relationship between these groups is not known (Best et al. 1998; Rosenbaum et al. 1997). Best et al. (1998) suggested that different migratory routes are used to each of these areas which would indicate considerable discreteness between them. There is substantial migration along the west coast of Australia (Chittleborough 1965). The specific breeding area is not well defined, though it is thought to be near Cape Leveque off the north coast of Australia (Jenner & Jenner 1994). There are potentially several destinations for animals migrating along the east coast of Australia. Breeding concentrations occur in the lagoon area inside the Great Barrier Reef (Chaloupka & Osmond 1999; Simmons & Marsh 1986) and off New Caledonia (Garrigue & Gill 1994), with some animals moving between this area and the east coast of

Australia (Garrigue et al. 2000). Breeding areas have also been reported off Tonga and in the Society Islands (Dawbin 1956; Gannier 2000). Exchange, or lack thereof, between breeding grounds in the Southern Hemisphere has not been well documented.

A special case occurs in the Arabian Sea, where both feeding and breeding occur in the same general area and whales are resident year-round (Mikhalev 1997; Reeves et al. 1991). Productivity is high in the area and is associated with monsoon driven current systems. Data from the region are too few to determine whether specific breeding sites occur there.

Migration

Migration allows individuals to utilise spatially discrete habitats. It has been defined in many, often contradictory ways (Baker 1978; Dingle 1996). Humpback whales undertake, long distance, seasonal return migration between two well defined high use habitats.

Migratory behaviour has evolutionary and ecological ramifications (Baker 1978; Dingle 1996; Peck et al. 1998; Rappole 1995). It is a response to variability in resource distribution and is favoured as seasonal variability in resource availability increases (Boyce 1991). The majority of migrants move between areas of high seasonal productivity to exploit seasonally available food supplies (Baker 1978; Dingle 1996; McCullough 1985; Rappole 1995). Many species, however, migrate to habitats which are not ideal for foraging, but meet other specific requirements. Many birds, for example, migrate to specific sites for their post-breeding molt, where shelter from adverse environental conditions and

protection from predators may be more important than food (Bollinger & Derksen 1996). Many primarily aquatic species must give birth on land, while some amphibious animals must lay eggs in water and thus must move away from food for breeding (Dingle 1996).

Because humpback whales fast on their breeding grounds, their low-latitude distribution is independent of productivity and is driven by other factors, presumably associated with the special requirements of reproduction. Because so little is understood about habitat requirements on the breeding grounds, the specific factors leading to migration are not clear (Clapham 1996; Corkeron & Connor 1999). It has even been suggested that the current pattern of migration reflects historic patterns of prey distribution, and that the utility of the migration been lost due to continental drift and the change in global climate (Lipps & Mitchell 1976). Migratory behaviour has been shown to change rapidly within a species, and is highly variable between closely related species (Rappole 1995), or even among adjacent, interbreeding groups in the same population (Boyce 1991) arguing against this interpretation. Within baleen whales there is intra-specific variability, with migratory and non-migratory groups of Brydes whales occurring in close proximity to one another (Best 1996). Further, migration is energetically costly and perhaps also dangerous, so a strong selective advantage must accrue in order to perpetuate it; long distance migration would rapidly be selected against unless it conveyed some current advantage.

Migration is observed in most of the mysticetes, with tropical or subtropical distribution in winter, and temperate or polar distribution in summer, though the precise winter range of many species is poorly defined (Lockyer &

Brown 1981). There are exceptions to the general pattern, with Bryde's whales remaining in tropical waters through the year, and bowhead whales rarely straying far from pack ice.

Because of their highly segregated seasonal habitats, migration is a prominent feature of humpback whale ecology. The migrations of some populations are among the longest for any mammal. Distances between the feeding and breeding areas may be as little as 1,200 km between California and Mexico in the North Pacific, though distances of between 3,500 and 6,000km are more typical. Extremes of around 8,000km have been reported in several areas (Table 1.1).

The migratory routes travelled by humpback whales are not well known except where they intersect coasts. They have traditionally been thought to consist principally of north-south travel between feeding and breeding areas at similar longitudes (eg. Mackintosh 1965). This has been broadly confirmed by the results of Discovery tagging and by re-sightings of naturally marked animals (Baker et al. 1986; Dawbin 1966; Kaufman et al. 1990; Stone et al. 1990), however numerous exceptions have now been documented (Darling et al. 1996; Dawbin 1964; Nishiwaki 1966; Stevick et al. 1999b). Recently, routes of individuals tracked by satellite telemetry have been shown to be quite direct over large distances (Mate et al. 1998), but little other information is available on routes at sea.

Similarly, the speed at which animals migrate is poorly known. The average speed of migration of two humpback whales tracked by satellite was 4.5km/hr (Mate et al. 1998) while the mean speed of migrating whales tracked by

theodolite from shore was 5.3 km/hr (Best et al. 1995). These speeds are consistent with the shortest recorded transit between migratory endpoints, which produced a minimum transit speed of 4.74 km/hr (Gabriele et al. 1996). It is also similar to the minimum travel speed of 4.3 km/hr for an individual which travelled 621km in 6 days in this study (Chapters 5 & 7). These figures suggest that extended transits are travelled at approximately 5km/hr.

Abundance, exploitation and protection

Exploitation

Since prehistoric times, whales were taken or scavenged opportunistically by seafaring and coastal people around the globe. The first regular commercial exploitation of whales for which we have records targeted the Balaenidae off the coast of Europe (Aguilar 1986; De Jong 1983; Scammon 1874; Scoresby 1820). The industry spread, first throughout the Atlantic, then globally (Allen 1980; Scammon 1874). Sperm whales became the principal target in the early 1700s and dominated the catch for 150 years (Mackintosh 1965; Rice 1989).

From the early development of whaling until the late 1800s whaling technology changed little, being principally based on operations from small rowing boats using hand harpoons and lances (Scammon 1874; Scoresby 1820). This approach limited the species that could be successfully exploited; animals which were too fast or powerful could not be captured. Humpback whales were taken by these early commercial whalers, but appear not to have been a primary target, at least when more valuable species were to be found. Their baleen was of lower quality than that of the right and bowhead, and they regularly sank when

killed, so the need to wait for them to begin decomposing and float before they could be retrieved and processed led to a higher loss rate than for some other species (Scammon 1874). None-the-less, thousands were taken throughout the world during the eighteenth and nineteenth centuries (Mackintosh 1965; Mitchell & Reeves 1983; Scammon 1874; Townsend 1935).

In the late 1800s whaling operations underwent dramatic changes with the advent of modern whaling. Humpback and blue whales were the predominant early targets of the modern fishery. Humpbacks were attractive commercially, as they were relatively easy to catch, and produced a high oil yield (Allen 1980). In many areas of the world, modern whaling initially concentrated on the taking of humpback whales; spectacular profits in the first few years led to rapid decimation of the stocks after which the fishery either closed or moved on to other, less valuable species (Mackintosh 1942; Tønnessen & Johnsen 1982).

The earliest modern whaling operations produced reported catches of around 1,500 humpback whales off the coasts of Norway, and 2,800 off Iceland between the 1860s and the 1920s, virtually exterminating humpbacks from these waters (Ingebrigtsen 1929; Sigurjónsson 1988; Tønnessen & Johnsen 1982). Catches of some 800 humpbacks during the 1920s, principally off west Greenland, Newfoundland and the West Indies, led to commercial extinction in the western North Atlantic as well (Mitchell & Reeves 1983; Tønnessen & Johnsen 1982). In the Southern Hemisphere catches peaked almost immediately after modern whaling commenced, with over 50,000 animals reported taken between 1909 and 1915, principally in the waters around South Georgia (Mackintosh 1942). In the North Pacific, 7,300 humpback whales were reported

taken off Alaska and California between 1905 and 1930 (Tønnessen & Johnsen 1982).

Officially reported catches may severely underestimate actual mortality. Not all killed whales were landed; as late as the 1950s struck and lost rates of 20-50% were reported (Tønnessen & Johnsen 1982). In addition, many vessels and companies were registered in countries not party to the International Convention for the Regulation of Whaling, and so were not bound by IWC regulations (Mackintosh 1965; Tønnessen & Johnsen 1982). As such, they were not required to submit records to the Bureau of Whaling Statistics. Further, it is likely that many vessels within the IWC operated with disregard for catching restrictions (Tønnessen & Johnsen 1982). Recent reports have demonstrated that the Soviet whaling fleet carried out widespread, indiscriminate whaling, falsifying records to make it appear that they were operating in compliance with catch restrictions (Mikhalev 1997; Yablokov 1994). Between 1947 and 1972, the Soviet fleet landed 48,651 humpback whales in the Southern Hemisphere while reporting only 2,820, with numerous catches in closed areas (Yablokov et al. 1998).

Thus hunting was carried out at high intensity throughout the range of the humpback whale, resulting in global depletion.

Protection

As a result of this overexploitation and evidence for depletion of stocks, taking of humpback whales was halted by the IWC in 1955 in the North Atlantic, 1963-64 in the Southern Hemisphere and in 1966 in the North Pacific (Best 1993). Humpback whales are listed as endangered under the United States

Endangered Species Act (NMFS 1991) and as vulnerable by the World Conservation Union (IUCN 2000).

Recovery

In some areas there is considerable evidence for recovery from depletion. Notably, surveys off Australia indicate an increase in the whales migrating off both the west and east coasts (Bannister 1994; Paterson et al. 1994).

In other regions where humpback whales were formerly abundant, there is little or no evidence for recovery. Near South Georgia, where 6,000 humpbacks were landed in a single season in 1910, recent ship surveys, land based sightings and opportunistic reports from mariners indicate that humpbacks remain rare today (Moore et al. 1999). Similarly, Best (1993), reports that surveys in the vicinity of Tonga indicate little recovery in that region, while the scarcity of sightings in the Cape Verde Islands in recent years is at odds with the former importance of the humpback whale fishery there (Hazevoet & Wenzel 2000; Townsend 1935).

In most regions the evidence is more equivocal. Published estimates are rarely made using the same sampling regime over the same area, nor are they analysed in similar ways. Thus differences between estimates may be the result of methodological differences rather than abundance changes. For example, the recently published estimate of 10,600 whales for the North Atlantic (Smith et al. 1999) is approximately an order of magnitude greater than the estimate of 785-1157 presented by Winn et al (1975). However, one is based upon capture-recapture analysis of identified individuals from throughout the North Atlantic,

the other on strip transects conducted on the principal breeding range making comparison between them suspect. Further, estimates of poor precision have low power to detect trends (Gerrodette 1987), and many estimates of abundance for humpback whales are of very low precision.

Furthermore, most surveys only cover a small part of the range of a population. While humpback whales show substantial site fidelity to feeding grounds, they have been observed to shift their distribution in response to prey availability (Payne et al. 1986; Whitehead & Carscadden 1985). Thus changes in abundance in regional surveys may reflect immigration or emigration related to prey abundance. Similarly, declines in one low-latitude area may represent a shift from one part of the breeding range to another. Since the primary determinant of distribution in the breeding range is conspecifics, whales are not likely to be equally distributed across all available habitat but will be aggregated. The geographical centre of the aggregation used by a population may shift, and such a shift may be more likely following disturbance or depletion (Clapham & Hatch in press). The evidence that humpbacks only recently began using Hawaiian waters for breeding may represent one example of this (Herman 1979), while the current scarcity of humpback whales in the Eastern Caribbean (Swartz et al. 2000) relative to their former importance in the region (Townsend 1935) may be another.

Estimates of abundance

The most precise estimate of abundance for any humpback population is that for the North Atlantic. Smith et al. (1999) recently estimated the abundance

of this population as 10,600 (9,300 – 12,100, see also Chapter 4). Calambokidis et al. (1997) recently estimated the abundance of the North Pacific population at approximately 6,000 animals. This estimate was based on re-captures between years in the breeding grounds. Similar breeding-breeding estimates from the North Atlantic have been shown to be biased by the difference in sex ratios within the sample (Palsbøll et al. 1997a; Smith et al. 1999). In addition, effort in Japanese waters was very low leading to possible biases in estimates from that area. The Scientific Committee of the International Whaling Commission recently estimated the abundance for the entire Southern Hemisphere south of 60° S at 10,000 (CV=0.27) based on sighting surveys (IWC 2000b).

Tables and Figures

Table 1.1 Examples of long distance migratory transits.

Feeding ground	Breeding ground	Identification method	Distance (km)	Reference
Bellingshausen Sea	Tonga	Discovery Tag	7,400	(Dawbin 1964)
Antarctic Peninsula	Colombia	Photo-id	8,334 *	(Stone et al. 1990)
Norway	West Indies	Photo-id	8,080	(Stevick et al. 1999b)
British Columbia	Japan	Photo-id	7,900	(Darling et al. 1996)

* The great-circle distance between the locations presented by Stone et al. (1990) is 7,590km. The published distance accounts for the necessity to travel around South America.

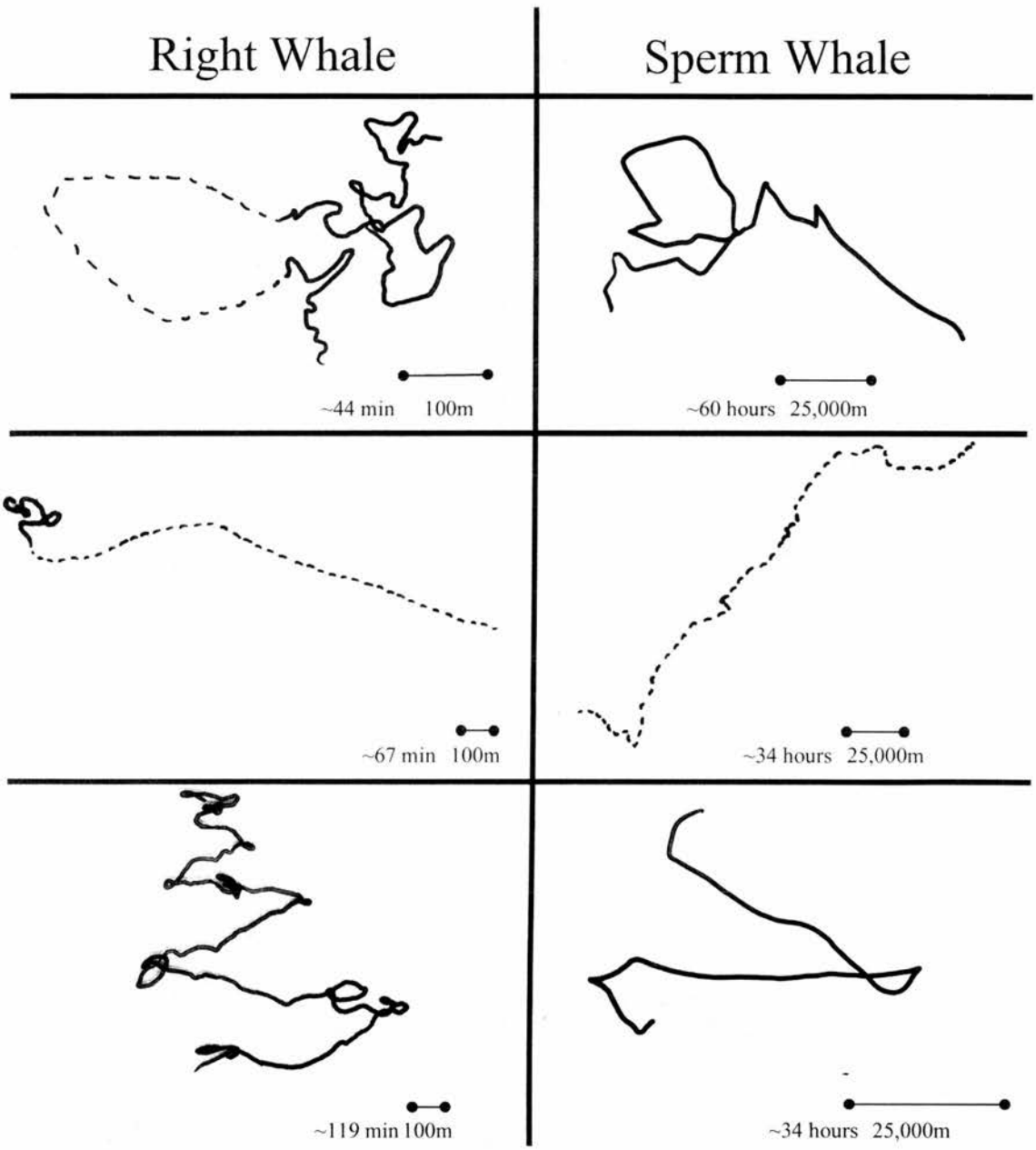

Figure 1.1. Foraging movements of right and sperm whales. Successful foraging , unsuccessful foraging . Approximate scale bars and duration of track given for each observation. Note the similarity in movement patterns between the two species in relation to foraging success in spite of the ecological differences between the two. Modified from Mayo and Marx (1990) and Jaquet and Whitehead (1999).

Chapter 2: Identification methods and databases

Identification by natural markings

Many characteristics of animals are individually variable, and in numerous species, individual animals are identifiable in the wild by variations in patterns of natural markings. This characteristic can be used as a natural tag. Recognition of individual animals from natural markings in the field or from photographs is an important tool for the study of animal populations and its use is widespread (Pennycuick 1978).

The use of natural markings for identification is non-intrusive, relatively inexpensive, and, since the animal is not handled, the behaviour of the animal is not altered by tagging, and the 'marking' can have no influence on the probability of recapture. On the other hand, markings must be unique, distinctive and stable relative to the time period of observations for the technique to be effective (Hammond 1986; Pennycuick 1978).

The applicability of natural markings as tags in a given situation depends upon the analysis for which the resulting data are to be used. The use of natural markings in identification of individuals has found wide application in studies of behaviour. Frequently in behaviour studies small groups of animals are observed. Thus the information content required to distinguish between individuals is smaller than in large populations. Also, animals are observed frequently, so it is easier to track animals in spite of mark change. Natural markings have also been

used for estimation of population parameters (Buckland 1990; Hammond 1986). For this purpose stability of markings between recapture periods is more important. High information content in markings is required to distinguish all animals in the group, though adaptations to account for poorly marked or 'unmarked' animals have been developed (eg. Wilson et al. 1999).

Identification by natural markings has been applied to the study of *inter alia*, reptiles (Hailey & Davies 1985; Sheldon & Bradley 1989), fish (Pot & Noakes 1985), birds (Bateson 1977; Bretagnolle et al. 1994; Scott 1978) and mammals (Briand Petersen 1972; Doolan & MacDonald 1997; Foster 1966; Hohmann & Fruth 2000; Jacobson et al. 1997; Karanth 1995; Miththapala et al. 1989; Moss 1996; Pennycuick & Rudnai 1970). It is common in studies of marine mammals. Natural markings have been used as tags on most all of the mysticetes (Agler et al. 1990; Darling 1984; Dorsey et al. 1990; Katona et al. 1979; Kraus et al. 1986; Payne et al. 1983; Rugh et al. 1992; Schilling et al. 1992; Sears et al. 1990; Tershy et al. 1990) and numerous odontocetes (Arnbom 1987; Bigg 1982; Flores 1999; Gowans & Whitehead 2001; Slooten et al. 1992; Würzig & Jefferson 1990; Würzig & Würzig 1977) and has also been applied to pinnipeds (Born & Knutsen 1997; Forcada & Aguilar 2000; Hiby & Lovell 1990; McConkey 1999) and sirenians (Anderson 1995; Moore 1956; Reid et al. 1991).

The earliest reported use of this technique in the study of marine mammals was by Moore (1956), who used sketches of body scarring on manatees to study behaviour patterns. In cetaceans, the technique was first used by Schevill & Backus (1960) who followed the movements of a humpback whale over ten days in 1958, recognising it in the field by dorsal fin shape, body

markings and fluke pattern. In the 1970s, due to increasing interest in the use of non-lethal and non-invasive methods to study marine mammals natural markings came into widespread use in studies of humpback whales (Baker & Herman 1981; Darling & Jurasz 1983; Glockner 1983; Juraz & Juraz 1979; Katona et al. 1979; Perkins & Whitehead 1977; Whitehead 1982; Whitehead et al. 1982; 1980).

Many features of humpback whales are individually distinctive; coloration patterns on the dorsal fin, flanks, ventral grooves, abdomen, pectoral flippers and flukes have all been used for identification, as have the shape of and irregularities in the flukes, dorsal fin, caudal peduncle and pectoral flippers, the number and location of throat grooves and scars occurring anywhere on the body (Blackmer et al. 2000; Glockner & Venus 1983; Glockner-Ferrari & Ferrari 1990; Katona & Whitehead 1981; Kaufman et al. 1987). The extent to which these features are useful for identification varies with the degree that they are visible to observers, particularly those at the surface, the level of variability in the markings and the stability of those markings over time (Blackmer et al. 2000; Carlson et al. 1990; Glockner & Venus 1983; Katona & Whitehead 1981).

The most commonly used feature for identification studies is the patterning on the ventral surface of the flukes (Katona et al. 1979; Katona & Whitehead 1981). Fluke patterns contain an enormous amount of information. Pigmentation ranges from nearly entirely white to fully black in a pattern which is probably inherited and shows considerable regional variation (Allen et al. 1994; Rosenbaum et al. 1995). Superimposed on this pattern are contrasting scars of various origins. The trailing edge is serrated. While the patterns can change,

sometimes dramatically, during the first year or so of life, they are remarkably stable thereafter (Blackmer et al. 2000; Carlson et al. 1990). The high rate at which humpback whales raise their flukes when diving assures that it is possible to identify a large proportion of individuals encountered using this method.

Markings on the flukes were the only marks used for identification in this study. Photographs of the ventral fluke surface were taken, generally from small boats (3-30m), using a wide range of camera and film combinations, though SLR cameras equipped with lenses of 200-300mm were most common. High-speed black and white film was used in most dedicated field projects. Photographs were taken from directly behind the whale to the extent possible and most were taken within a range of 100m. Prints of these photographs were compared manually to the best available photograph or photographs (catalogue photographs) of all previously identified whales to identify re-sightings. Where photographs were confirmed to be re-sightings, the existing identification number was applied to the new sighting, and the catalogue photographs updated if required. Those which were not identified were compared a second time. Where practical, the second comparison was conducted by a different individual. Resources did not allow comparison to the full collection a second time, so the second comparison was made only to those regions between which re-sightings were most commonly found in previous years. Some photographs were compared using the computer-assisted method devised by Mizroch et al (1990) in addition to manual comparison, and all photographs were digitally archived. Records for all photographs and related sighting information are maintained in a relational database system.

Genetic tagging

DNA extracted from tissue has enormous information potential, and may be used as a method for identifying individuals (Gill et al. 1985). The potential application of this method to studies of cetaceans was discussed by Amos and Hoelzel (1990). The DNA fingerprinting techniques in use until recently, however, were cumbersome and expensive and the process was not widely used. Recent advances in molecular genetics have made it possible to identify individuals from genetic markers isolated from tissue samples reliably and inexpensively enough to use this technique as another form of natural tag (Palsbøll et al. 1997a)

For this study, genetics data were available on the genotype at six nuclear microsatellite loci. These data were used to identify individual humpback whales. Skin biopsy samples were collected using a modified dart fired from a 68kg draw crossbow. The 40cm dart was fitted with a hollow tip 8mm in diameter with internal barbs to retain the sample, and had a moulded float which also acted to limit penetration of the dart. Details of sampling equipment, techniques and sample handling are presented by Palsbøll et al. (1991) and Smith et al. (1999).

While biopsy sampling is invasive, the samples collected are small, and so physical injury is unlikely. Sampling equipment is sterilised to prevent infection. No long term and little short term reaction has been reported from biopsy collection (Brown et al. 1994; Clapham & Mattila 1993; Gauthier & Sears 1999; Weinrich et al. 1991). Indeed several authors have noted that reactions to close approaches by the sampling vessel are very similar whether a sample is taken or not.

The projects

There are two major projects involving individual identification of humpback whales which have geographic coverage over substantial regions of the North Atlantic: the Years of the North Atlantic Humpback Whale project (YoNAH) and the North Atlantic Humpback Whale Catalogue (NAHWC). The following analyses draw upon both to varying extents.

YoNAH

The YoNAH project, an ocean-basin-wide study of humpback whales, was conducted in the North Atlantic during 1992 and 1993 (Smith et al. 1999). As part of this study, photographic and genetic samples were collected from humpback whales in all of the major feeding grounds and the West Indies breeding ground (Figure 2.1). Sampling within each region was organised by individuals familiar with the local density and distribution of humpback whales. Intensity of sampling was allocated in proportion to expected density on the basis of previous information regarding whale abundance and thus was primarily distributed in regions of highest whale concentration as indicated by previous sighting surveys, published and unpublished records, though in some areas it was additionally constrained by logistical considerations (Smith et al. 1999). Sampling was conducted using standardised protocols for locating groups of whales, systematically covering groups once located, and maximising the chances of successfully sampling each individual encountered and were thus designed to minimise biases due to sampling effort. Once whales were sighted, the nearest group of whales was engaged. These whales were followed until all

individuals in the group were identified, the group was lost, or 45 minutes had elapsed. The field team then moved to the nearest group until all or most of the whales in the area had been sampled. Further details of field sampling protocol, survey effort, data collection, and laboratory methods are provided by Smith et al. (1999).

Photographic analysis was conducted at College of the Atlantic, Bar Harbor, Maine, USA. The YoNAH photographic database contains records of 4297 photographic sampling events representing 2987 individuals. Biopsy samples were collected during 2135 sampling events representing 1834 unique individuals. Genetic analyses were conducted at the Genetic Institute, University of Copenhagen, Copenhagen Denmark and at the University of Bangor, Gwynedd, UK. Following Smith et al. (1999), photographs or biopsy samples of an individual collected on different days are considered separate sampling events while multiple samples collected on the same day are not. Results presented here do not precisely follow Smith et al. (1999), as a small number of additions and corrections have been made subsequent to publication.

The YoNAH photographic data were the primary source used in these analyses because of the ocean-basin-wide coverage, the availability of accurate location information, the greater sampling intensity leading to large sample sizes and the more representative sampling effort. Unless otherwise stated analyses presented here are based upon this sample.

NAHWC

The NAHWC is a central curation facility for identification photographs of humpback whales from throughout the North Atlantic Ocean. The collection is housed at College of the Atlantic, Bar Harbor, Maine, USA. It contains photographs from a total of 11,551 photographic sampling events representing 4,873 individuals. Photographs date from 1952, though few data are available before 1978 and comparison is not complete subsequent to 1991. The project is collaborative; photographs were submitted by more than 350 contributors. Samples were collected opportunistically, so temporal and spatial coverage is highly variable (Figure 2.2). Most feeding ground samples were collected in the western North Atlantic; few samples were available from Iceland and waters farther east. Techniques for photographic handling and comparison are detailed in Katona and Beard (1990).

Photographic quality

Because photographic quality can influence the ability to recognise individual animals, all photographs were coded for quality, but the coding criteria for the two collections were different, with the YoNAH standard applying only to image quality, while the NAHWC standard combined photographic quality and distinctiveness of markings. Thus the two are not directly comparable. The YoNAH standards were applied to a subset of the NAHWC results for consistency in the analysis of abundance trends (Chapter 4). Analyses where re-sighting rates were compared were made on the basis of only

good quality photographs to minimise biases related to differences in photographic quality between samples.

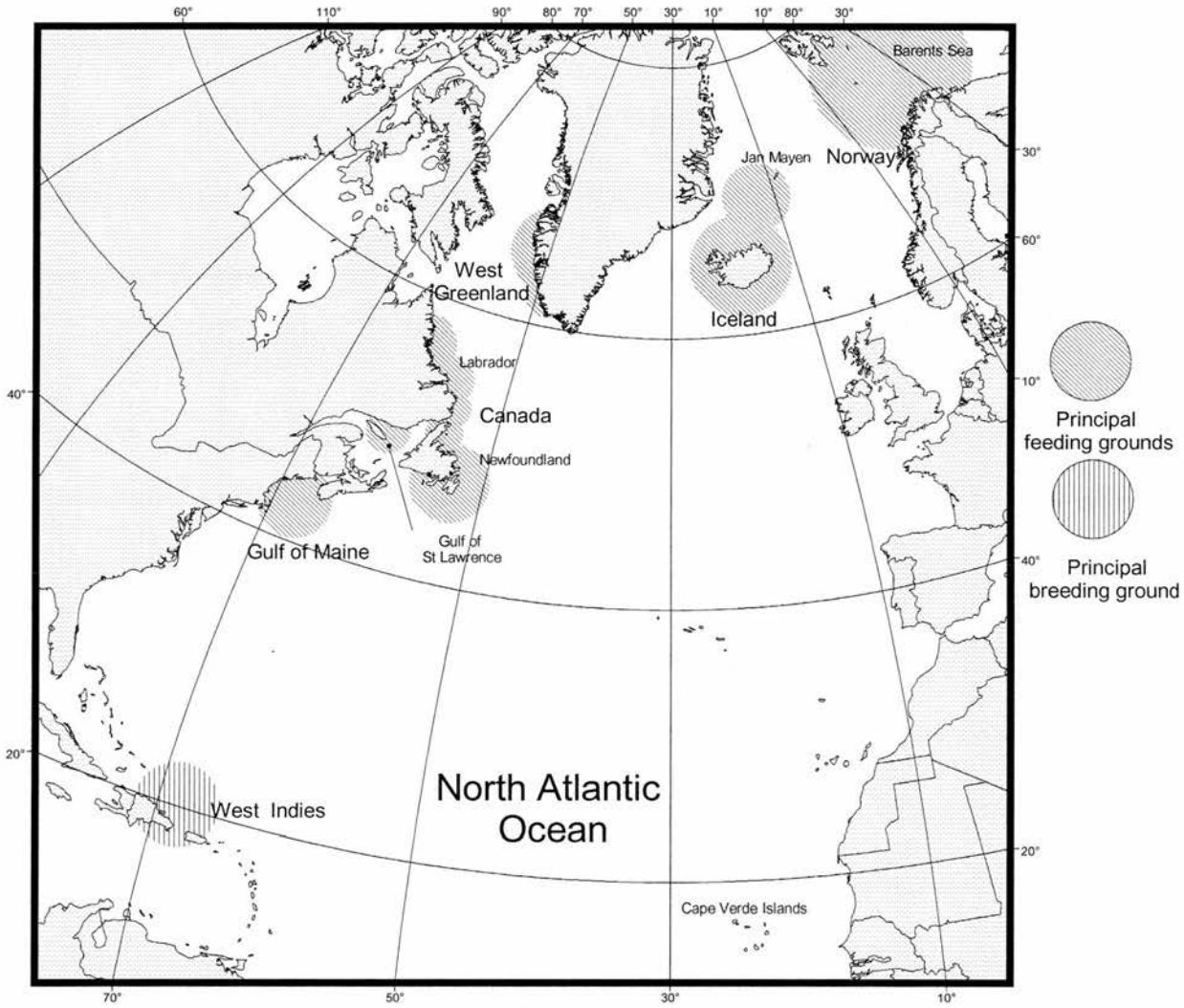

Figure 2.1. Map of the North Atlantic Ocean showing the principal areas of seasonal humpback whale concentration and locations mentioned in the text.

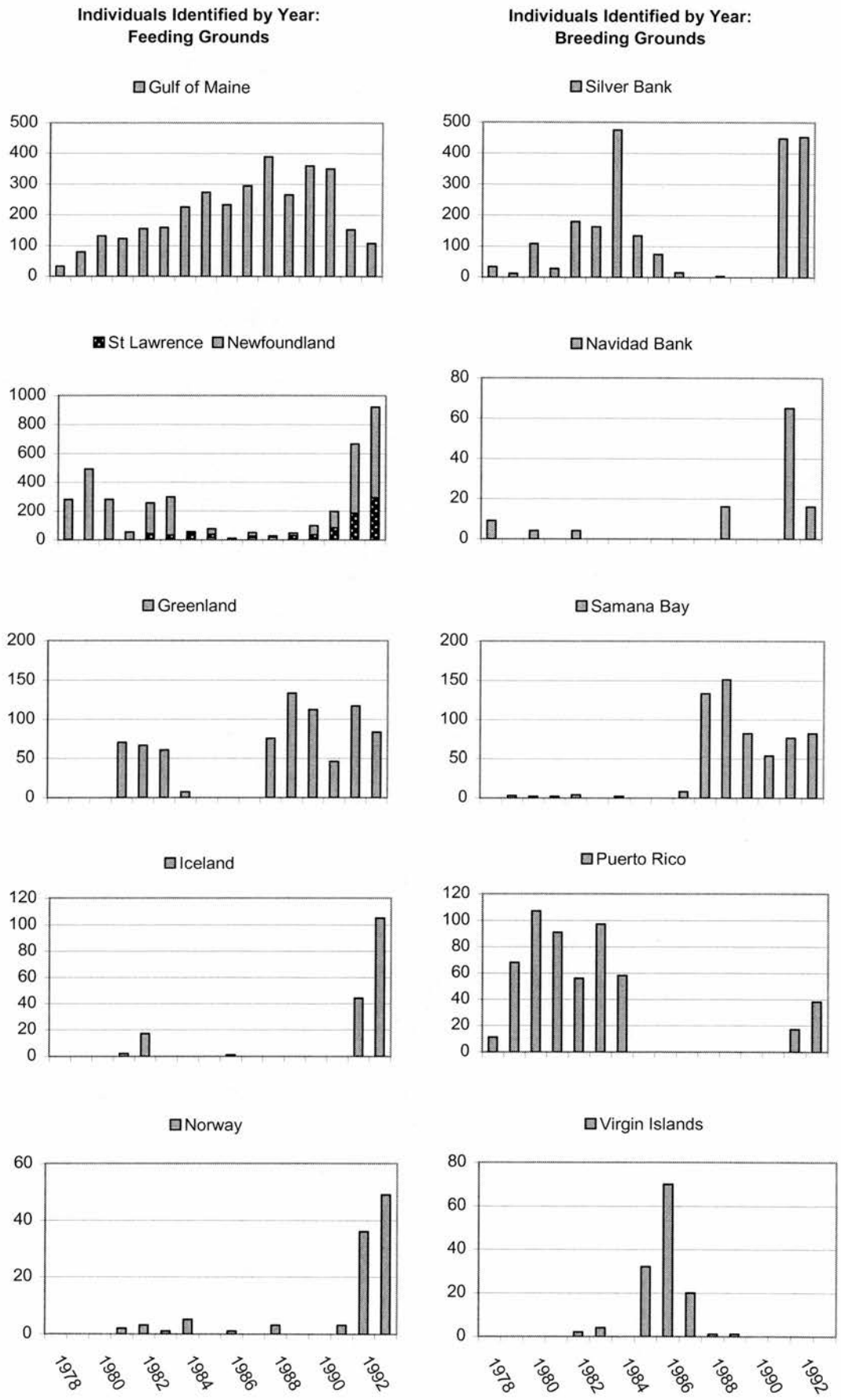

Figure 2.2. Geographical distribution of identified whales by year.

Chapter 3: Errors in identification using natural markings: rates, sources and effects on capture-recapture estimates of abundance

Summary

The results of a double marking experiment using natural markings and microsatellite genetic markers to identify humpback whales confirm that natural markings are a reliable means of identifying individuals on a large scale. Of 1,410 instances of double tagging there were 414 re-sightings. No false positive and 14 false negative errors were identified. The rate of error increased with decreasing photographic quality; no errors were observed among photographs of the highest quality rating while an error rate of 0.125 was identified in sightings for which less than half of the fluke area used for identification was visible. There was also a weaker relationship between error rate and the distinctiveness of markings, which may result from non-independence in coding for image quality and distinctiveness. A correction is developed for the Petersen two-sample abundance estimator to account for false negative errors in identification and a parametric bootstrap procedure for estimation of variance. In application to abundance estimates from the North Atlantic, the correction reduces the bias in estimates made using poorer quality photographs to a negligible level.

Introduction

Recognition of individual animals from natural markings is an important tool for the study of animal populations and is widely applied to diverse taxa (eg. Bretagnolle et al. 1994; Miththapala et al. 1989; Pot & Noakes 1985; Sheldon & Bradley 1989). It is common in studies of marine mammals, particularly cetaceans, with application to most of the mysticetes and numerous odontocetes (for a review of methods see Hammond et al. 1990a) and is also applied to pinnipeds (Forcada & Aguilar 2000) and sirenians (Reid et al. 1991). Widespread application of this technique to cetaceans has dramatically increased our understanding of population parameters, movement, behaviour, abundance and structure in many whale populations (eg. Smith et al. 1999; Wade & Clapham in press; Wilson et al. 1999). Capture-recapture studies using naturally marked animals are appropriate in situations where capture and restraint are difficult or where there is concern about disturbance of the study population (eg Forcada & Aguilar 2000; Karanth & Nichols 1998), and thus may be one of the few feasible methods of estimating abundance for some endangered species.

The likelihood of errors in individual identification has been recognised since the early development of the technique (Bateson 1977; Payne et al. 1983). Incorrect identification may involve falsely identifying two sightings of different individuals as the same (a false positive error) or two sightings of the same individual as different (a false negative error). Errors may be the result of poor quality photographs or observation conditions (Agler 1992; Bateson 1977; Forcada & Aguilar 2000; Friday et al. 2000), the lack of distinctiveness of the individual markings (Friday et al. 2000; Payne et al. 1983; Pennycuick & Rudnai

1970; Sheldon & Bradley 1989) or the lack of stability in markings over time (Bretagnolle et al. 1994; Carlson et al. 1990; Dufault & Whitehead 1995; Sheldon & Bradley 1989). While the problem of identification errors has long been recognised, it has proven fairly intractable; few data on the causes or extent of identification error have been reported.

The use of individual identification for capture-recapture estimates of abundance is based on several assumptions, which have been discussed extensively elsewhere (Hammond 1986; Pollock et al. 1990; Seber 1982). Among them are the assumptions that no animals lose their marks during the study, and that all marked animals are reported on recovery. Bias due to tag loss and non-reporting can be severe (Arnason & Mills 1981; Pollock et al. 1991; Seber 1982; Seber & Felton 1980).

Identification errors are in some respects similar to tag loss, though they are not equivalent. In tag loss, a captured individual is recorded as unmarked when it should be marked. This is irreversible and is a cumulative process, with increasing total loss, and often increasing rate of loss with time (Diefenbach & Alt 1998; Stobo & Horne 1994). Visible features can change over time (for example see Bretagnolle et al. 1994; Carlson et al. 1990) and changes which rendered an individual unrecognisable would be the equivalent of tag loss. With most identification errors, however, the individuals remain marked but the marks are not recognised. This is more similar to non-reporting than to tag loss. Previous studies of non-reporting, however, have emphasised reporting rates by hunters, anglers or commercial fishermen, so the marked animals are removed from the population and are not available for further re-capture (Pollock et al.

1991; Stobo & Horne 1994). In errors of identification of naturally marked animals, however, an individual remains in the population and is incorrectly identified as two nominal individuals. The problem of overlooked or unrecognised recaptures of animals that remain in the population and may be subsequently re-captured has received little attention.

Double marking experiments can be used to estimate tag retention rates (Diefenbach & Alt 1998; Seber 1982; Seber & Felton 1980; Stobo & Horne 1994) and rates of non-reporting (Pollock et al. 1991; Stobo & Horne 1994). However, double marking has rarely been applied to studies of natural markings. Previous attempts at double marking experiments with cetaceans have used natural markings on two areas of the body, one of which is generally less variable than the primary region, and have had limited sample sizes available (Gowans & Whitehead 2001; Payne et al. 1983). Recent advances in genetic techniques, notably the use of microsatellite loci, have made it possible to identify individual animals on a large scale on the basis of genetic markers (Palsbøll et al. 1997a). Thus the use of genetic and natural markings in the same population provides two independent sources of identification and an opportunity to examine identification errors.

I report here on the results from a large-scale double-marking experiment in which humpback whales (*Megaptera novaeangliae*) were identified by both natural and genetic markers. This is the first extensive double-marking experiment on a cetacean species. It is also the first large-scale test of errors in individual identification by natural markings for any species. I show that natural markings may be successfully used to identify large numbers of individuals over

large spatial scales. I also develop a correction for the two-sample Petersen estimator to account for errors in identification and demonstrate that this correction reduces or eliminates bias resulting from re-sighting errors.

Methods

Data Collection

Data reported here were collected as part of the Years of the North Atlantic Humpback whale project (YoNAH), an international collaborative effort to study the population biology of the humpback whale throughout its range in the North Atlantic Ocean (Chapter 2, Smith et al. 1999).

Individual identification photographs were taken of the pigmentation pattern, and scars on the ventral side and contours in the trailing edge of the tail flukes (Katona et al. 1979). Protocols for handling of photographs and photographic identification are detailed in Chapter 2. Because the quality of the photograph may influence recognition of individual whales, all photographs were given a quality designation based on the clarity and contrast of the image, and the angle of the fluke to the camera. Quality codes range from excellent (1) to acceptable (3), with category 3 images further subdivided into 3+ and 3- based on the extent to which information was obscured by image quality. Photographs showing only the right or left sides of the fluke were designated as half flukes, while images showing less than about 20% of the fluke area were designated as partial flukes because of the difficulty in re-identifying animals based on only part of the tail being visible. These half and partial flukes are occasionally referred to as quality 4.

Distinctiveness of the individual markings may also influence recognition. Each nominal individual was therefore given a distinctiveness rating ranging from very distinctive (1) to poorly marked (3) based on the colour pattern, scarring and serrations in the trailing edge. Details of the coding process, and definitions of the coding criteria are presented by Friday et al. (2000). Additionally, since right and left halves could not be matched to one another, including both in the same sample will artificially decrease recaptures. Therefore, abundance estimates based on samples which included half flukes were calculated separately excluding right halves and excluding left halves.

Skin biopsy samples were collected for genetic analysis as described by Smith et al. (1999). Photographs and biopsy samples were obtained from the same individuals whenever possible. Total-cell DNA was extracted using standard protocols (Maniatis et al. 1982). Genotype was determined at one tri-nucleotide and five tetra-nucleotide nuclear microsatellite loci as described by Palsbøll et al. (1997b).

Location of errors

Identifications resulting from natural markings and from genotype were entered into a relational database along with associated data on sampling location and time. When discrepancies between identifications made by genetic and photographic means were located, the photographs were re-examined to determine whether an error occurred. Discrepancies could result from either false positive or false negative errors in either photographic or genetic identification.

Errors may be made during comparison between sightings within a sampling period as well as between samples.

Genetic errors relevant to this sample are discussed elsewhere (Palsbøll et al. 1997a) and are not considered further here. Where discrepancies existed but identification was unambiguous, these discrepancies were designated as non-matching errors in which the photographs and biopsy samples from one of the sightings were incorrectly associated with one another either in the field or during some stage of handling or analysis.

Correction of abundance estimates

A modification was developed for the standard two-sample Petersen mark-recapture abundance estimator to account for false negative errors in identification. Matching protocols make false positives highly unlikely, and none were observed (see below).

Within a sample, i, failure to match animals identified at different times will erroneously increase the number of individuals n_i which is identified from the overall number of identification events s_i. This occurs because a single individual is erroneously treated as two individuals. To account for this, the true value of the number of individuals identified in sample i, n'_i, is derived as follows.

Let: s_i = the number of identification events during sample i,

n_i = the number of unique individuals in sample i,

(therefore, $s_i - n_i$ is the observed number of re-sightings

during sample i),

a_i = the true number of re-sightings in sample i,

e_i = the false negative error rate for sample i.

Then:

$$s_i - n_i = a_i(1 - e_i)$$

and:

$$\hat{a}_i = \frac{s_i - n_i}{1 - e_i}.$$

Therefore, an estimate of the true number of individuals identified in sample i is:

$$n_i' = s_i - \hat{a}_i$$

$$= \frac{s_i(1 - e_i) - s_i + n_i}{1 - e_i}$$

$$= \frac{n_i - e_i s_i}{1 - e_i}.$$

When matching between samples, failure to match individuals present in both samples will erroneously reduce the number of recaptures. The observed

number of recaptures, m_2, needs to be corrected by the false negative error rate for matching between samples individuals, e_m.

In addition, there is a small chance that a false negative match within a sample could coincide with a false negative match between samples. In this case, a further modification is needed, because an identification missed within a sample will not influence the number of recaptures. The corrected m_2 must therefore be reduced by the sum of the proportional errors in each sample, $(n'_i - n_i)/n_i$. Note that this secondary correction ignores the unlikely possibility that the same error occurs in both samples, and will normally be at least one order of magnitude less than the primary correction.

The true number of recaptures between samples is thus estimated as:

$$m'_2 = \left(\frac{m_2}{1-e_m}\right)\left(1-\sum_{i=1}^{2}\frac{n'_i-n_i}{n_i}\right).$$

The modified Petersen estimator is then:

$$\hat{N}' = \frac{n'_1\, n'_2}{m'_2}.$$

From which Chapman's modification (Seber 1982) can be calculated as:

$$\hat{N}' = \left(\frac{(n'_1+1)\,(n'_2+1)}{m'_2+1}\right) - 1.$$

Photographic error rates are related to image quality. Therefore the false negative error rate for sample i, e_i, is estimated, stratified by image quality as:

$$\hat{e}_i = \sum_{j=1}^{c} p_{ij} f_j,$$

where c is the number of photographic quality classes, f_j is the false negative error rate for photographic quality class j, and p_{ij} is the proportion of identification events in sample i, s_i, represented by photographs of photographic quality class j.

The error rate applicable to recaptures between samples, e_m, is a function of the number of individuals, n_i, not the number of identification events. It is thus estimated as:

$$\hat{e}_m = \sum_{j=1}^{c} \frac{n_{1j} + n_{2j}}{n_1 + n_2} f_j.$$

Estimation of variance and confidence intervals

No closed-form for is available estimating the distribution of abundance estimates which incorporates all of these bias corrections and accounts for the uncertainty in error rate estimates. Thus, variance of the modified estimator was estimated by re-sampling using the parametric bootstrapping procedure presented in Appendix 1. The standard error was calculated from 1000 estimated values of N', and the 95% confidence interval was estimated using the bias-corrected percentile interval method (Efron and Tibshirani 1993).

Results

During 1992 and 1993, 4,297 photographic samples and 2,326 biopsy samples were collected. Following Smith et al. (1999) identifications of the same individual on separate days were considered separate identification events. There were 1,410 instances of double tagging. Of these there were 414 cases in which double-tagged animals were re-identified by one method or the other (or both) during another identification event, so that identification by the two methods could be compared. A total of 88 discrepancies between photographic and genetic identifications were found, in 37 cases the photographic identifications were the same and the genetic identifications different, and in 51 cases the reverse was true.

Errors Identified

By far the largest source of discrepancies was the failure to link photographs and biopsies correctly; 74 non-matching errors were identified. These could have resulted in the field from confusion over the identity of the whales sampled within a group, to difficulty in interpreting field notes during initial data analysis or to mis-labelling of biopsy samples or photographs, to handling errors in the lab or even to typographical errors. The average group sizes from which non-matching errors were identified (3.06 whales/group) were larger than those of double-tagged animals from which no discrepancies were identified (2.73 whales/group). The distributions were significantly different (Mann-Whitney U=91,244, p=0.0018), suggesting that confusion of animals is more likely to occur in larger groups.

No false positive errors were identified.

A total of 14 false negative errors was identified. Of these, five were based on sightings represented only by half or partial fluke photographs. Of the remaining nine, four cases were based on sightings with photographs that, while meeting minimum quality standards, were exceedingly difficult to match to one another because of differences in angle, contrast, clarity or portion of fluke visible. The information in these photographs was consistent with them coming from the same individual, and they are recorded here as photographic errors. Some ambiguity remains in the identifications, however, and the possibility that some are non-matching errors cannot be entirely ruled out.

Table 3.1 shows the relationship between errors identified and the image quality and individual distinctiveness ratings. While the number of observations in each cell is small, error rates increase steadily with decreasing image quality. They range from no errors identified for quality 1 photographs to over 12% for half and partial photographs. The range of error rates varies less between distinctiveness categories than between photographic qualities. Within distinctiveness categories a relationship with photographic quality is apparent in spite of the small sample sizes in each cell.

Since error rates are related to image quality, for the rates determined in the double marking experiment to be an accurate representation of overall error rates in the sample, the double-tagged individuals should be representative of the distribution of image quality in the sample as a whole. The experimental sub-set is nearly 10% of the overall photographic sample, and most photo quality and

distinctiveness classes are also very close to 10% of those overall except in cases where sample sizes are small.

Estimates of Abundance

Four estimates of humpback whale abundance in the North Atlantic Ocean were recently presented by Smith et al. (1999). These were based on one winter sample from the low latitude breeding range and one summer sample from the high latitude feeding range (see Chapter 4). They were not corrected for identification error. However they were restricted to photographs of quality 3+ or better to minimise error related bias (Friday et al. in press). Table 3.2 presents these four estimates along with the calculated error rates, estimates and proportional bias (uncorrected/corrected) for corrected estimates using the same photographic quality selection for comparison. Because there were no false positives identified in the double marking experiment, all biases in abundance estimates are positive. The proportional biases are highly consistent among the four estimates ranging only from 1.040 to 1.041. This is true in spite of considerable variability in re-sighting rates, recapture rates and image quality between samples and estimates. Precision of the corrected estimates is slightly lower than that of uncorrected estimates. Much of this difference is the result of the bootstrapping process; the precision of corrected and uncorrected estimates is comparable if both are determined through bootstrapping (Table 3.2).

Errors lead to substantial increases in uncorrected abundance estimates as photographs of progressively poorer quality are included in the sample (Figure 3.1a). The increase in proportional bias with inclusion of quality 3+ images is

similar to that with inclusion of quality 3- or quality 4 (half and partial photographs), even though the number of samples included in the latter categories is only about a third of that in the former, and thus the effect might be expected to be substantially smaller. Application of the correction to these estimates substantially reduces the variability in estimates made with different photographic qualities, effectively eliminating this bias (Figure 3.1b).

Sensitivity analysis demonstrated that the error correction is not influenced by absolute abundance or recapture rates provided that the error rates and within sample re-sighting rates remain the same. Biases are sensitive, however, to variability in re-sighting rates (Figure 3.2). Higher re-sighting rates inflate bias, but not appreciably at the error and re-sighting rates reported here.

Discussion

Comparison of results from photographic and genetic identification confirms that natural markings provide a reliable means of identifying individuals on a large scale. While errors in identification will cause inflation of abundance estimates if not taken into account, the error rates for photographic identification reported here are low relative to other sources of variability in recapture rates. Further, knowledge of the error rates allows for a correction to be applied.

While the error rate is low, the relatively large number of non-matching errors suggests that considerable care should be given to ensuring that samples and photographs are linked correctly to sighting records, particularly where group sizes are large. Care is especially important when information gained from

genetics is associated with other information associated with photographs, or when identifications by the two methods are combined for a single analysis. Fortunately, non-matching errors do not reflect upon the reliability of identification by natural markings and they have no impact on capture-recapture estimates of abundance made by any single identification method.

False Positive Errors

It has been observed that false positive errors produce large biases in estimates of population parameters, and that they are especially problematic in large collections where they may cause substantial biases in two sample estimators even at low rates (Gunnlaugsson & Sigurjónsson 1990). Schwartz and Stobo (1999) examined the influence of false positive errors on open population models. Errors were caused by mis-reading of tags, which resulted in high false positive rates (0.10, SE 0.015) but no false negatives. Large biases in parameter estimates were observed, with capture probabilities overestimated by between 4% and 34%. Thus it is reassuring to find no evidence of false positive error in this experiment.

However, risk aversion to false positives inevitably increases the number of false negatives, and the balance between these factors has not been investigated in practice. The theoretical basis for concern over the influence of false positive errors assumes that these errors are equally likely in each comparison made (Gunnlaugsson & Sigurjónsson 1990). In practice, the likelihood of a false positive error is a function of the similarity of the markings of the individuals compared. Thus, if the information content on which

identification is based is high, the number of comparisons at risk for false positive errors is correspondingly low.

The lack of false positive errors in photographic identification shown here probably reflects the caution displayed in matching protocols. Previous experimental results have suggested that false positives are likely in photographic identification. Carlson et al. (1990) reported a range of false positive errors in identification of humpback whales from 0.0053 to 0.0951, while a similar experiment on fin whales, where markings are more difficult to identify, reported a false positive rate ranging from 0.015 to 0.187 (Agler 1992). In both studies error rates were related to the experience of the personnel undertaking the matching. These experiments, however, examined the decisions of a single individual. In practice, matching protocols are generally risk averse to false positives. Identifications are made by experienced individuals, use restrictive criteria for re-identification and/or are confirmed by at least two individuals, substantially reducing the probability of errors (Agler 1992; IWC 1990; Katona & Beard 1990; Kraus et al. 1986; Payne et al. 1983; Rugh et al. 1992). In the results presented here, all identifications were checked by at least two experienced staff, and cases where information was inadequate or where consensus could not be reached were resolved in favour of not matching.

False Negative Errors

False negative errors are well known to occur in studies of natural markings (Agler 1992; Bateson 1977; Carlson et al. 1990). Carlson et al. (1990) reported false negative error rates in recognition of humpback whales among

experimental subjects ranging from 0.0075 to 0.0233. Agler (1992) found a false negative error rate of 0.107 for fin whales among the most experienced personnel. The relative obscurity of markings in fin whales compared with humpbacks makes it difficult to compare results between species. Forcada and Aguilar (2000) identified no errors in comparison of multiple photographic sightings of 14 individuals monk seals also marked with artificial tags, yet they showed considerable bias in estimates made with the poorest quality photographs, indicating the presence of such errors in their data. These experiments were conducted on small sets of photographs, while it has been suggested that the rate of errors is a function of fatigue and will therefore increase with increasing catalogue size (Gunnlaugsson & Sigurjónsson 1990).

Both photo quality and distinctiveness appear to be related to error rates, and both may play some role in the making of errors (Table 1). No errors were identified among those sightings with the best quality photographs regardless of the distinctiveness rating of the individual. Among whales with the highest distinctiveness rating, errors were only identified among half and partial photographs. However, the strong correlation between image quality and error rate, with a virtual doubling of error rate with each sequential decline in quality designation, and the less evident trend between error rates and distinctiveness ratings indicate that image quality is a more important determinant of error rate than is distinctiveness. Further, it has previously been shown that distinctiveness coding may be a function of image quality (Friday et al. in press). Thus the increase in error rate with decreasing distinctiveness rating may indirectly be the result of image quality.

Pattern change has been implicated in error rates (Carlson et al. 1990; Gowans & Whitehead 2001; Wilson et al. 1999), however, none of the errors identified here was the result of pattern change. Changes in ventral fluke patterns of humpback whales are extremely uncommon, and occur most often in young animals (Blackmer et al. 2000; Carlson et al. 1990).

Samples represented only by photographs coded as right or left halves or as partial accounted for five of the 14 errors identified, giving an error rate of over 12%. This indicates that, even among animals given high distinctiveness ratings, photographs which do not show all of the fluke area are subject to higher rates of identification error, even when a considerable amount of information is present in the area photographed.

Influence on Estimates of Abundance

Our results show that errors in identification positively bias abundance estimates. Even if not accounted for, however, bias due to identification errors proved small compared to the variability between estimates and the precision of the estimates. This bias can be substantially reduced but not eliminated by removing the poorest quality photographs (Figure 3.1). This is normally the approach adopted in capture-recapture studies using natural markings. The four cases of errors from images rated as acceptable, but where matching was none-the-less ambiguous, indicate that not all errors can be eliminated where photographic quality is poor, even with nearly perfect photographic comparison. These errors could be eliminated, or nearly so, by implementing more stringent

photo quality standards. However, this would substantially reduce the sample size and thus result in loss of precision.

Knowledge of error rates specific to image quality allows corrections to be made that virtually eliminate the bias resulting from identification errors. This allows inclusion of more samples, improving precision of abundance estimates while introducing negligible bias.

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Tables and Figures

Table 3.1. Distribution of error rates by photo quality and distinctiveness. Figures in parentheses are numbers of errors observed and the sample size for each category. Assuming that errors are a function of the poorest image in the comparison rather than both, this table presents the distribution of only the sighting with the poorest quality images. Where distinctiveness ratings disagreed, images were compared to determine the correct rating. Totals for photographic quality columns do not equal the sums of those columns as some individuals were given a distinctiveness code of Unknown.

		Photographic quality					
		1	2	3+	3-	4	Total
Distinctiveness quality	1	0	0	0	0	1.00	0.028
		(0, 23)	(0, 39)	(0, 7)	(0, 1)	(2, 2)	(2, 72)
	2	0	0.033	0.026	0.125	0.083	0.030
		(0, 66)	(4, 121)	(2, 77)	(1, 8)	(2, 24)	(9, 296)
	3	0	0	0.222	0	0.091	0.073
		(0, 8)	(0, 12)	(2, 9)	(0, 1)	(1, 11)	(3, 41)
	Total	0	0.023	0.043	0.091	0.125	0.034
		(0, 97)	(4, 172)	(4, 94)	(1, 11)	(5, 40)	(14, 414)

Table 3.2. Comparison of corrected and uncorrected estimates of abundance of humpback whales in the North Atlantic Ocean during 1992 and 1993. Uncorrected estimates are those presented by Smith et al. (1999). Corrected estimates and bootstrap standard errors are calculated using the methods presented in the text. Bias represents the proportional bias (uncorrected/corrected). Both corrected and uncorrected estimates are made with Chapman's modification and include only images of qualities of 3+ or better to be comparable with Smith et al. (1999). Analytical variance of uncorrected estimates calculated as given in Seber (1982). For each sample the observed and corrected sample sizes and the calculated error rates are presented. For each estimate the observed and corrected number of recaptures are presented.

Sample	S	n	e	n'
Winter 1992	683	629	0.0248	627.6
Summer 1992	1,024	787	0.0224	781.6
Winter 1993	623	582	0.0257	580.9
Summer 1993	1,293	937	0.0200	929.7

Estimate	n'_1	n'_2	M_2	e_m	m'_2
W_{92}- S_{92}	627.6	781.6	39	0.0219	40.2
W_{93}- S_{93}	580.9	929.7	52	0.0209	53.6
W_{92}- S_{93}	627.6	929.7	48	0.0206	49.5
W_{93}- S_{92}	580.9	781.6	48	0.0224	49.5

	Not Error Corrected					Error Corrected			
		Analytical		Bootstrap			Bootstrap		
Estimate	Abundance	SE	cv	SE	cv	Abundance	SE	cv	Bias
W_{92}- S_{92}	12,410	1,828	0.147	2,095	0.159	11,930	1,961	0.159	1.040
W_{93}- S_{93}	10,320	1,300	0.126	1,454	0.134	9,910	1,361	0.134	1.041
W_{92}- S_{93}	12,060	1,595	0.132	1,871	0.146	11,580	1,676	0.143	1.041
W_{93}- S_{92}	9,370	1,229	0.131	1,418	0.143	9,160	1,268	0.138	1.040

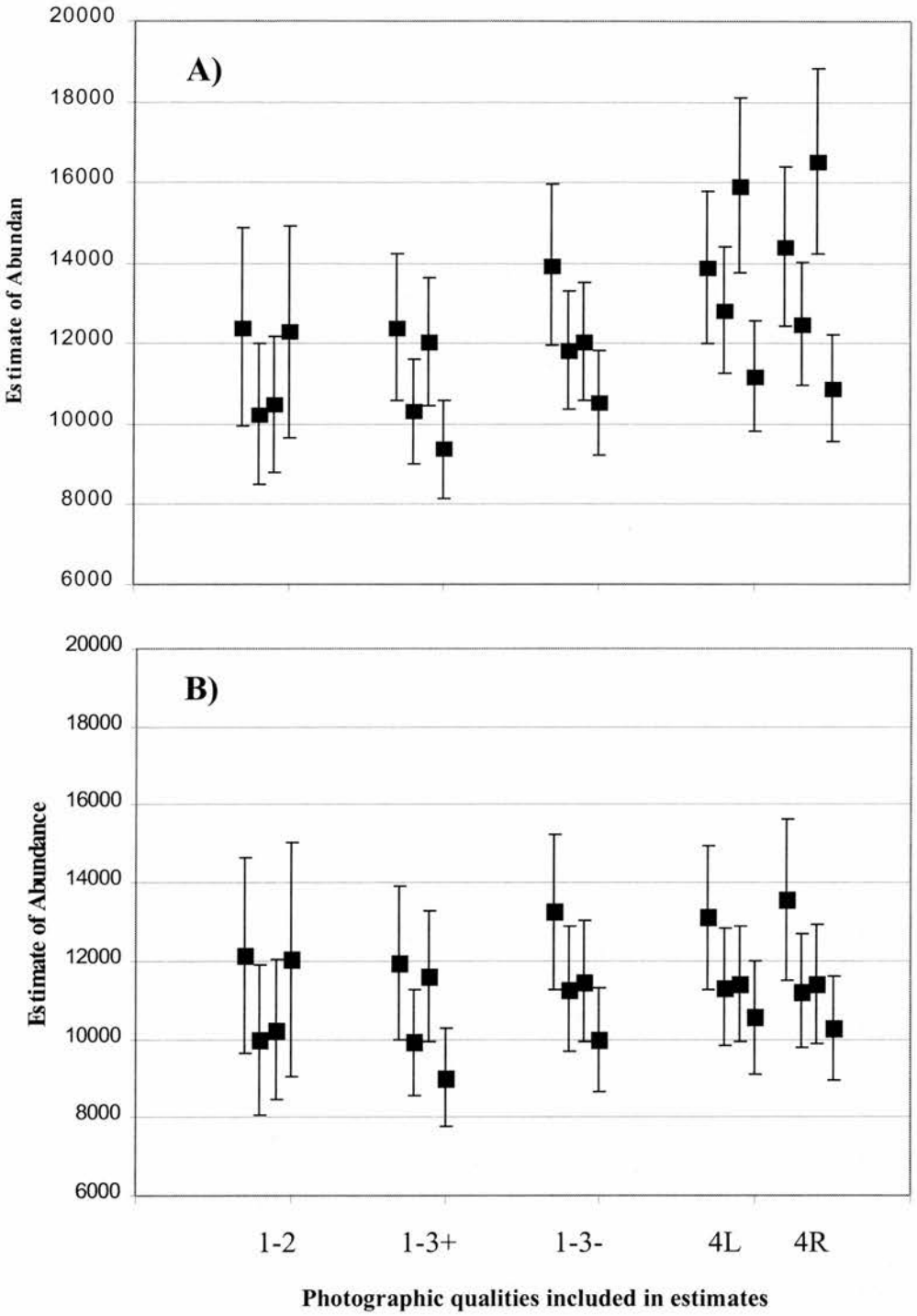

Figure 3.1. Change in four breeding-feeding estimates of abundance for North Atlantic humpback whales from the YoNAH project (Smith et al. 1999) with inclusion of photographs of decreasing quality (±standard error). Photographic quality categories after Friday et al. (2000). A) uncorrected estimates, and B) estimates incorporating the correction for identification errors. Category 4 includes photographs coded as half or partial for each combination of samples one estimate is made excluding right halves (4L) and another excluding left halves (4R).

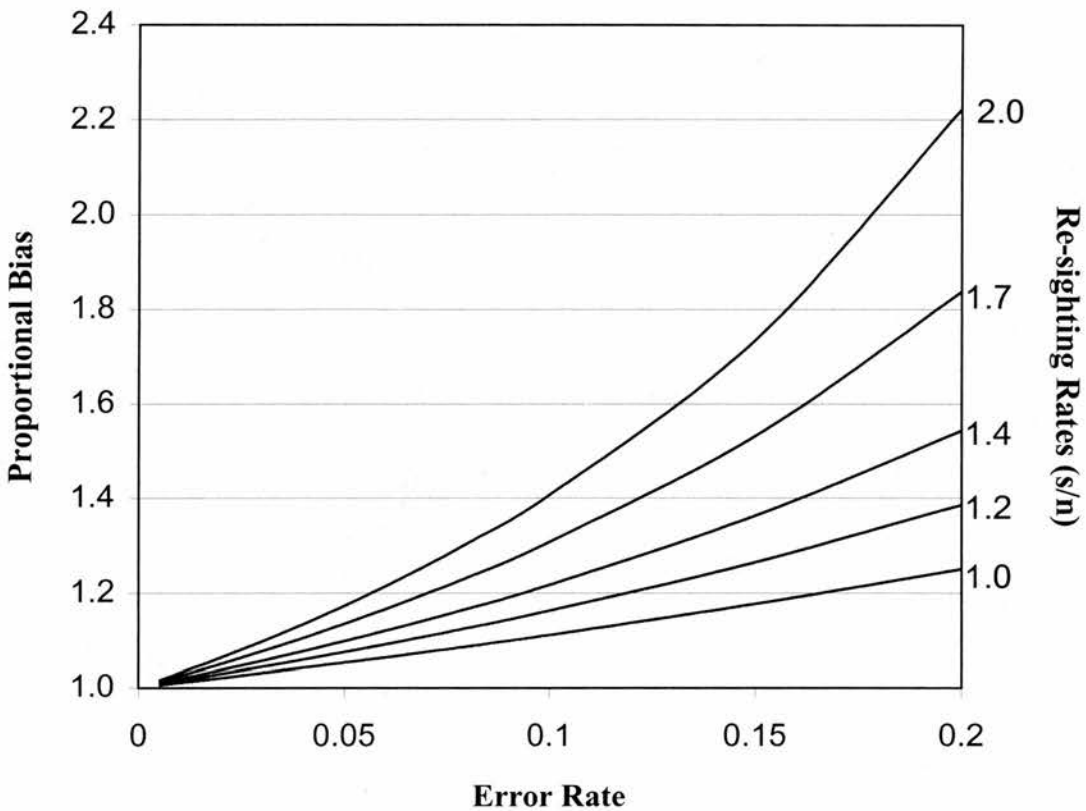

Figure 3.2. Effects of error rates on proportional bias in estimates of abundance. Curves represent different re-sighting rates. Results are insensitive to variability in recapture rate. Approximate resighting rates from the YoNAH project are 1.1 for breeding ground samples and 1.3 for feeding ground samples.

Chapter 4: Trends in Abundance of North Atlantic Humpback Whales, 1979-1993

Summary

I present here an assessment of trends in abundance of humpback whales in the North Atlantic Ocean based upon capture–recapture estimates of abundance using naturally marked individuals. A total of 24 estimates was calculated spanning 14 years. Estimates ranged from 6,920 to 12,640 with CVs from 0.07 to 0.39. These estimates are larger and more precise than those previously published from similar time periods using largely the same data. The estimate of 11,570 (95% CI 10,290-13,390) for 1992 and 1993 is based on several methodological improvements upon preliminary estimates published from these data. It represents the most current and best available estimate of abundance for the North Atlantic Ocean. The estimated rate of increase over the 14 years was 0.042 (SE=0.004; r^2=0.83).

Introduction

Humpback whales were an early target of the modern pelagic whaling industry, and were one of the predominant species taken from the 1860s to the early 1900s. High levels of hunting mortality led to rapid declines throughout their range; in most areas, stocks were severely depleted within a few years of the advent of commercial operations (Tønnessen & Johnsen 1982). Commercial hunting was stopped by the International Whaling Commission in the North

Atlantic in 1955, the Southern Hemisphere in 1963-1964 and in the North Pacific in 1966 (Best 1993; Mackintosh 1965).

It is widely assumed that populations of humpback whales have made substantial recoveries since the end of hunting. However, this is difficult to document. In some areas high rates of increase have been reported (eg. Bannister 1994), while in others there is no evidence of recovery (eg. Moore et al. 1999). Humpback whales remain listed as endangered under the United States Endangered Species Act of 1973 (NMFS 1991) and vulnerable by the World Conservation Union (IUCN 2000) and are listed on Appendix 1 of the Convention on International Trade in Endangered Species (www.cites.org).

Humpback whales are long-lived, have relatively low reproductive capacity, are widely distributed, and capable of large-scale movements. Thus assessment of abundance trends requires long time series of data over broad geographic areas. Assessment of abundance over entire ocean basins has not previously been attempted, however, due to the resources required. I present here an assessment of trends in abundance for the North Atlantic Ocean over 14 years based upon capture–recapture estimates of abundance using naturally marked individuals.

Humpback whales in the North Atlantic

Though they were not the primary target of early fisheries, a substantial number of humpback whales were taken in the North Atlantic over several hundred years by a combination of Yankee pelagic whalers and small-scale coastal operations (Mitchell & Reeves 1983; Townsend 1935). Catches of

approximately 1,500 animals by early modern whaling operations off Norway (Ingebrigtsen 1929), 2,800 off Iceland (Sigurjónsson 1988), and smaller numbers off Ireland, the Hebrides and other parts of northern Europe (Thompson 1928; Tønnessen & Johnsen 1982), appear to have almost completely exterminated humpbacks from the eastern North Atlantic by the very early 1900s. In Newfoundland waters they were severely depleted by the 1920s (Mitchell & Reeves 1983; Tønnessen & Johnsen 1982). Takes of small numbers of individuals continued in some areas until legal hunting ended in 1955 (Mitchell & Reeves 1983), while catches for research purposes occurred off Canada in 1969-1970 (Mitchell 1973) and aboriginal takes continued in Greenland until 1985 (IWC 1986) and are ongoing in the eastern Caribbean (IWC 2000a).

With such a long history of exploitation, the total take and pre-exploitation status of the humpback whale in the North Atlantic are difficult to ascertain. Humpbacks were depleted by such an early date that catch records from many areas are incomplete or even absent. Assessment of pre-hunting abundance is extremely difficult, therefore, and the accuracy of any resulting estimates remains uncertain (see Mitchell & Reeves 1983).

These problems may be exacerbated by the existence of illegal and unreported catches. Widespread, often indiscriminate, catches have been reported globally. The best documented of these were catches made by the Soviet fleet (Mikhalev 1997; Yablokov 1994; Yablokov et al. 1998; Zemsky et al. 1995). It is likely, however, that non-compliance with IWC regulations was widespread, and fleets under several flags operated outside of the IWC altogether (Mackintosh 1965; Tønnessen & Johnsen 1982). While there is not evidence in the Soviet

records suggesting widespread takes of humpback whales in the North Atlantic (P. Clapham, pers. comm.), Yablokov et al. (1998) state that 'Soviet whaling fleets... used to begin hunting whales immediately after passing the Suez Channel (sic), *Gibraltar, and exiting from European coastal waters*' (emphasis mine). They list the region of the Canary Islands and off west Africa as an area where large numbers of unreported catches were made, though the species taken there are not specified. Thus, undocumented takes of humpback whales may have occurred during transits of the North Atlantic by whaling fleets bound for the Southern Hemisphere at least until 1972 when an international inspection programme was implemented.

With 45 years since the end of commercial hunting, some level of recovery is likely to have occurred, but there are few data available to substantiate or quantify this. Regional estimates do suggest that populations are increasing, perhaps at a substantial rate. Sigurjónsson and Gunnlaugsson (1990b) present a rate of increase of 0.138 (annual rate 14.8%) for humpbacks off Iceland over a twenty year period between 1968 and 1988. This rate is higher than is probable given the biological parameters of this species (Clapham et al. 2000), however, and the authors suggest that immigration could account for some of this change. Barlow and Clapham (1997) present a rate of increase of 0.063 (annual rate 6.5%) for humpback whales from the Gulf of Maine based on an inter-birth interval model. Estimates of abundance for west Greenland increase between 1988 and 1993 but the trend is not significant (Larsen & Hammond 2000). These are regional studies, however, and the rates of increase are not necessarily representative of the North Atlantic as a whole. Katona and Beard (1990) present

estimates of abundance for the western North Atlantic between 1979 and 1986, with a reported rate of increase of 0.094 (annual rate 9.9%), however the precision is low and this result is not significantly different from 0.

Methods

Individually distinctive markings on the ventral surface of the tail flukes allow identification of individual humpback whales (Katona et al. 1979). There are currently two large collections of identification photographs covering extensive areas of the North Atlantic, the North Atlantic Humpback Whale Catalog (NAHWC), and the Years of the North Atlantic Humpback Whale (YoNAH) project (Chapter 2). I combine these two sources to examine abundance trends from 1979-1993.

The NAHWC is a central curation facility for fluke photographs collected throughout the North Atlantic, though substantially biased toward the western North Atlantic (Katona & Beard 1990). It contains records of approximately 11,500 sightings of nearly 5,000 individual animals collected as early as 1959, though with most effort occurring after 1978. Data used here were collected between 1979 and 1991.

The YoNAH project was conducted during 1992 and 1993. YoNAH investigators collected individual identification photographs from all of the known major concentrations of humpback whales in the North Atlantic using protocols designed to minimise biases due to sampling (Smith et al. 1999). This collection contains approximately 4,300 sightings of just under 3,000 individual whales.

Generating abundance estimates

In order to maximise both precision and consistency, standard methods were applied to all samples and for all estimates. Precision of the individual estimates will influence the power of the analysis to detect trends (Gerrodette 1987). Bias will influence estimation of trends if the level of bias varies between estimates. The use of biased estimates may be acceptable in the estimation of trends provided the level of bias is consistent among all estimates used in the study.

As humpback whales are found in two quite distinct seasonal habitats, the photographs from each year form two distinct samples, one from the high latitude summer feeding grounds, and the other from the low latitude winter breeding ground. Heterogeneity of capture probabilities results in biases in capture-recapture estimates of abundance (Hammond 1986; Pollock et al. 1990; Seber 1982). The probability of capture is not uniform for humpback whales, but the sources of heterogeneity are different in the feeding and breeding grounds.

Heterogeneity in breeding ground samples appears to be largely a function of gender differences in behaviour and migration (Chapter 4; Brown et al. 1995; Palsbøll et al. 1997a; Smith et al. 1999). The level of bias which results will, therefore, be a function of the gender ratio in the sample. There are few data available that would allow us to evaluate the gender ratios of individuals sampled in the West Indies prior to YoNAH, nor is there reason to believe that this ratio was consistent over all years. Thus estimates based upon two breeding ground samples are certain to be biased. While it is possible that these biases are

consistent over time, there is little evidence to support or refute this, and so their use in trend assessment is suspect.

Heterogeneity in feeding ground samples is a function of the site fidelity demonstrated by individual animals and the distribution of effort relative to abundance (Hammond 1986; 1990; Smith et al. 1999). As the spatial distribution and intensity of sampling in feeding areas is known to vary greatly between years (Figure 2.2), this bias is also unlikely to be consistent across samples, and is likely to lead to biased trend estimates.

The sampling biases in the feeding and breeding areas appear to be independent, however, and thus estimates based on one feeding ground sample and one breeding ground sample should be less biased (Smith et al. 1999).

One difficulty in evaluating trends from these data is the variable and often quite small sample sizes, particularly from the West Indies. For many of the years, samples are small enough that only one or two recaptures are made between successive sampling seasons. Low numbers of re-captures not only result in poor precision of abundance estimates, but also in biases in those estimates, and these are particularly likely when less than 7 re-captures occur between samples (Seber 1982). Of the 25 estimates which can be generated from the NAHWC data using successive single sampling seasons, 15 result in less than 7 recaptures. Thus the majority of the single season samples result in estimates for which bias may be expected.

The variability of estimates may be partially overcome by calculating means of several estimates, though these means may be strongly influenced by

estimates of low precision or severe bias. Precision based weighting of means can account for variation in precision. In capture-recapture estimation, however, abundance and variance are estimated from the same data and are not independent. Because of this relationship, estimates below the true abundance will receive more weight than those above it, leading to negative bias in weighted means. Also, because the relationship between estimates of variance and abundance is not linear, low estimates will receive weighting disproportionate to estimates that are high by the same magnitude. Thus, single season estimates are prone to bias because of small sample sizes and means of these estimates are prone to bias from weighting methods.

An alternative approach that increases sample sizes without introducing additional sources of bias is to pool samples, thereby increasing sample sizes. In order to retain the feeding-breeding estimator, I pool the feeding ground samples from two consecutive years and the breeding ground samples from two consecutive years and calculate abundance from these pooled samples. The sampling period may start either with a winter season or a summer season and run for four consecutive sampling periods. This results in much larger sample sizes, greater precision and less likelihood of bias.

This treatment eliminates much of the variability in point estimates (Figure 4.1). It also dramatically improves the precision of the estimates; the CVs for pooled estimates are comparable to those from means of four estimates based upon single year samples from the same period, and the bias due to lack of population closure is also similar between these two approaches (see below). The bias from small recapture numbers is reduced by such pooling, though it is not

entirely eliminated. Only 3 of the 24 (12.5%) of the estimates calculated in this manner were based upon fewer than 7 recaptures as compared with 15 of 25 (60%) for estimates based upon sampling from single years. As a result, all estimates used here were calculated using such pooled data.

Generating trends

Two models were fitted to these data. In the first model the intrinsic rate of increase in the population, r, is constant over time, t, thus exponential growth at a constant rate is assumed:

$$N_t = N_0 e^{rt}.$$

In order to investigate the possibility of a change in population growth rate over time, a logistic model was also fitted. This is given as:

$$N_t = \frac{N_0 e^{rt}}{1 + N_0 (e^{rt} - 1)/K}.$$

This assumes that the rate of increase declines as the population approaches some asymptotic abundance, K, (Hastings 1997). Because of the small number of samples, the fit of the two models was compared using the second order bias adjustment to Akaike's Information Criteria (AIC_c) (Burnham & Anderson 1998).

To account for the degree of variability in the precision of abundance estimates, estimates were weighted by the inverse of the CV^2. This gives a measure of precision that is less strongly correlated with abundance than is the variance, and thus is less likely to bias the regression toward low estimates.

Photographic quality

The quality of images used in identification has been identified as a potentially important source of bias in abundance estimates (Chapter 6, Friday 1997; Hammond 1986). Since the quality of photographs may vary between areas and years based on both the experience of the photographers and the sampling or environmental conditions under which photographs are taken, this bias cannot be assumed to be constant over time. All photographs from 1992 and 1993 were coded for image quality by the criteria presented by Friday et al. (2000). For earlier years, only the best photograph from the breeding ground and the best from the feeding grounds each year were coded for quality due to resource limitations.

Abundance estimates are made using the modified Petersen estimator presented in Chapter 3 to account for identification errors. This correction is stratified by the distribution of photographic quality in the sample. Because not all sightings are coded for quality, the false negative error rate within each sample, e_i, could not be calculated in the manner proposed in Chapter 3. Instead, e_i was calculated using the distribution of photographic qualities for individuals rather than sampling events in sample i. This will result in a slight under-estimation of n'_i, and a resulting over-estimation of abundance. Both error rates

were applied to the YoNAH samples and indicated a difference in n' of about 1.5% for feeding ground samples and 0.013% for breeding ground samples.

Also, because some sightings have unknown photographic quality, it is not possible to use the parametric bootstrap procedure presented in Appendix B. Instead, the analytical variance was calculated using the Chapman's formula (Seber 1982) and the corrected values of n'_1, n'_2 and m'_2 (see Chapter 3). These variance estimates are lower than the corresponding bootstrapped variance by about 10% using the YoNAH samples.

These two factors introduce unknown variance components to the estimates. The observed proportional bias between the bootstrapped and analytical variances presented ranged from 1.09-1.13 for the four single year YoNAH estimates, while differences of n' of the magnitude observed change abundance estimates by less than 1%.

To investigate the sensitivity of the trend estimate to the effect of this unknown variance, a simple simulation was conducted. The variance of each estimate was modified by a percentage selected at random from a normal distribution, estimates and variances were log-transformed, and the standard error of the slopes of the resulting inverse variance-weighted linear regressions were calculated over 1,000 replicates.

For variances modified by a mean of 0.1 and a standard deviation of 0.05, approximately the same mean, though with somewhat greater variability than that observed in the results from 1992 and 1993, the standard error was only 1.40×10^{-4}. Doubling the mean and standard deviation increased the standard error

only slightly to 1.46×10^{-4}, while increasing the variability to 0.5 (sd 0.2) only resulted in a standard error of 4.53×10^{-4}, suggesting that these factors have little influence on the estimation of trends from these data.

In order to use the most consistent data in estimating trend, the estimates from 1992-1993 used in the trend analysis were calculated in the same manner as the other estimates, though a superior estimate for those years is available as shown below.

Results

Five abundance estimates were generated for the 1992-1993 samples using the full error correction and the bootstrap estimate of variance. These were based on different combinations of photographic qualities (Table 4.1). Application of the Mean Square Error procedure presented by Friday et al. (in press) indicated that the optimal balance of bias and precision was obtained through inclusion of all photographs of whole flukes but exclusion of photographs showing half of the flukes or less. All estimates used in trend analysis were calculated using this combination of photographic qualities for consistency.

A total of 24 estimates was calculated spanning 14 years (Table 4.2). These used the modifications outlined above necessitated by the limited available information on photographic quality. Estimates ranged from 6,920 to 12,640 with CVs from 0.07 to 0.39. These estimates are larger and more precise than those from similar time periods and using largely the same data presented by Katona and Beard (1990) and by Smith et al. (1999). Comparison between the NAHWC

and YoNAH collections has not been conducted, so estimates between 1991 and 1992 are not available.

Four consecutive estimates spanning 1990 and 1991 were anomalously lower than those from any adjacent intervals (Table 4.2); values this extreme seem improbable given the precision of the estimates. To examine this, I excluded these points and fitted an un-weighted linear regression to the remaining (log transformed) estimates. The expected value for each time interval was calculated from this regression. The probabilities of obtaining the expected values, given the observed values and standard errors, assuming a lognormal distribution, were all <0.0001.

Stevick et al. (1999b, see also Chapters 6, 7) showed that sighting date in the West Indies was related, in part, to high latitude origin. Humpback whales from the eastern North Atlantic are seen in the West Indies significantly later than those from the west. Only one individual from Norwegian waters was identified in the West Indies prior to February 19, with most appearing later (Stevick et al. 1999b). This introduces a possible source of heterogeneity in capture probabilities that is common to the breeding and the feeding ground samples. This will result in bias in abundance estimation using the feeding-breeding estimator.

Two of the suspect estimates used the 1990-1991 winter sample; the other two used the 1989-1990 winter sample. Sampling in these seasons was conducted earlier than in any other winters during the study. During 1990 and 1991, no sampling was conducted after February 18, while for the 1989-1990 sample only 26% of individuals were sampled after this date, and less than 10% after

February 25. In contrast, no other winter sample had less than 30% of whales identified later than February 18. Thus individuals from the eastern North Atlantic are likely to be substantially under-represented in the winter samples for all four of these estimates. As no samples from Iceland or Norway were obtained during any of the feeding ground samples used in these four estimates, eastern whales are also under-represented in the summer sample.

In order to investigate the relationship between sighting dates in the West Indies and the calculated abundance estimates, the mean sighting dates in the West Indies for each estimate were plotted against the residual (observed estimate - the predicted abundance based on the un-weighted regression excluding the suspect estimates). There was no obvious relationship between abundance estimates and the mean sampling dates for the West Indies sample on which they were based, with the notable exception of the four anomalous estimates outlined above. These were based upon the earliest West Indies samples and had the largest residuals (Figure 4.2). The correlation for the remaining points was not significant (correlation coefficient = -0.328, df 17, ns).

To further examine the relationship between sighting date and re-capture rate, samples of 200 individuals each were selected at random from the 1992-1993 West Indies sample. These years were selected because of the large sample size, high sampling intensity and coverage over much of the West Indies season. The number of individuals with feeding ground records was compiled for each of 200 replicate samples. Feeding ground re-captures from Iceland and Norway were excluded to more closely approximate high latitude sampling for years preceding 1992. The relationship between the number of recaptures and mean

West Indies dates was weak but significant; there was considerable variability in the number of individuals re-sighted across the range of mean dates (correlation coefficient = -0.210, df 198, $p<0.01$).

Because of the weakness of this relationship when sampling occurred throughout the season, I compared the number of re-captures between samples from the West Indies selected randomly from all dates, and samples selected only from the first half of the West Indies season (prior to Feb 19). Samples of 200 individuals were selected from the 1992-1993 West Indies sample. In contrast to the weak relationship for sampling over the entire season, these results were dramatic. Over 200 replicates, this resulted in a mean of 4.84 more recaptures in the early samples than in the samples taken across the entire season ($t=7.59$, $p = 1.2 \times 10^{-12}$). Thus the number of re-captures is biased upward (proportional bias 1.231) if samples are collected only early in the breeding season and there is no sampling in Iceland and Norway. If this bias is applied to the number of recaptures observed during the 1989-1991 period and a standard Chapman's estimator calculated, three of the four estimates corrected in this manner fall approximately where the regression predicts them, while only one remains substantially low (Figure 4.3). Thus, bias of the magnitude observed in these estimates is consistent with bias generated by restriction of sampling to the early breeding season during those pairs of years. The precision of the resulting correction factors, however, is poor. Thus the four estimates which use the 1989-1990 and the 1990-1991 West Indies sample are not used in analysis of the rate of increase.

Rate of increase

Both the exponential and logistic growth equations fit these data reasonably well. The ΔAIC_c value was 2.8. As the lower AIC_c value is for exponential growth, the model with the fewer parameters, this model is the most parsimonious.

The estimated instantaneous rate of increase was 0.0420 (SE=0.0044; r^2=0.831). This corresponds to an annual rate of increase of 4.29%. The use of variances that are artificially small will produce overly optimistic standard errors in estimates, however, the simulation suggests only a slight increase to 0.0045. If increase had occurred constantly at this rate since hunting ended in 1955, the population at that time would have been about 2,500.

Discussion

The results presented here represent the first long-term estimates of the trend in abundance for humpback whales across an ocean-basin. Since individuals from all feeding areas in the North Atlantic are known to occur in the West Indies in winter at similar rates (Chapter 6), the estimates presented here represent the abundance of humpback whales from across the entire North Atlantic. There have been few previous attempts to conduct long-term monitoring of humpback whale abundance. Bannister (1994) and Patterson et al. (1994) used estimates of migratory concentrations near the west and east coasts of Australia, respectively, to estimate abundance change. In both areas, a substantial portion of the population is believed to migrate coastally, and thus these may represent estimates of the growth rates for entire populations. At least

in east Australia, however, there is uncertainty about the breeding ground destination of these animals, which may utilise several breeding areas (Dawbin 1966; Garrigue et al. 2000), and thus it is not entirely clear what this trend represents. Other estimates of trends are all based upon localised groups (eg. Barlow & Clapham 1997; Chaloupka et al. 1999; Sigurjónsson & Gunnlaugsson 1990b). These rates may be thus be biased by immigration or emigration, or may not be representative of ocean-basin trends.

The existence of animals that do not use the West Indies as a breeding ground will produce bias in these estimates, however. Given what has been observed in other oceans, it is unlikely that animals utilising different breeding areas move randomly between them (Baker et al. 1986; Chittleborough 1965; Darling & Mori 1993; Dawbin 1964; Perry et al. 1990; Urbán R et al. 2000). Thus individuals using other breeding areas will be available to be sampled in high latitudes but will not be present in the West Indies. Some animals are known to occur in winter outside the principal breeding range in the West Indies, most notably in the Cape Verde Islands (Hazevoet & Wenzel 2000). Differences in nuclear genetic markers between Iceland and other regions in the North Atlantic support the existence of more than one breeding group, and indicate that the exchange between these groups is low on an evolutionary time scale (Valsecchi et al. 1997). Current evidence suggests that the number of individuals not using the West Indies is small. Relatively few individuals have been sighted in the Cape Verde Islands (Hazevoet & Wenzel 2000; Reiner et al. 1996), and the difference among feeding areas in rates of re-sighting to the West Indies is not adequate to be detected statistically with the sample currently available (Chapters

6 & 7). Thus, while this bias cannot be quantified, it is likely to be small. Further, since the proportion of individuals using any other areas is not likely to change from year to year, this bias will be consistent and therefore should not influence the trend reported here.

These results demonstrate that the sampling biases in high and low latitudes are not completely independent as is assumed in the feeding-breeding estimator. Instead, the feeding ground origin of animals sampled in the West Indies is related in part to the timing of the West Indies sampling. They further show that this non-independence may influence abundance estimates. This effect appears to be minimal provided sampling occurs over much of the breeding season. It may cause substantial biases, however, where sampling is restricted to part of the season, particularly early or late in the breeding season.

All of these estimates are subject to bias due to lack of population closure. Both recruitment and mortality occur between samples, while the pooling of samples means that the population is subject to mortality and natality during a sampling period as well. We can approximate the extent of this bias. Hammond (1986) showed that Petersen estimates for a population subject to both death and recruitment were positively biased from population size at the time of the first sample by approximately the recruitment rate divided by the survival probability. In simulations based upon YoNAH sampling subject to mortality and recruitment, Friday (1997) showed that winter-summer estimates within a year were effectively un-biased relative to the population at the time of the first sample. Estimates that included samples from multiple calendar years, however, were biased by approximately the sum of the mortality rate and the rate of

increase, a factor similar to that proposed by Hammond (1986). Friday (1997) further showed that this bias was similar whether the samples spanned six months or 18 months since both of these combinations included recruitment from only one year. Extensions of these simulations comparing estimates made using pooled samples and un-weighted means of four separate estimates for the same time period show that the lack of population closure during sampling has little effect (N. Friday, pers comm). The biases are very similar; the bias in estimates made from pooled samples is about 0.2% larger than that for the corresponding mean. This similarity is to be expected because the mean time elapsed between samples is six months in both cases. Simulations show the bias using pooled samples to be approximately half of the sum of the mortality rate and the rate of increase. For rates of increase below 5% it is somewhat less than half, while at higher rates of increase it is slightly more than half (N Friday, pers comm).

Two estimates of survival rate are available for the North Atlantic; both are based upon re-sighting results from the Gulf of Maine. Buckland (1990) estimated a survival rate of 0.951 (0.929-0.969), while Barlow and Clapham (1997) using an expanded version of the same database estimated a survival rate of non-calves of 0.960 (se=0.008). Utilising the rate of increase calculated here, and applying the rate of bias indicated by Friday's simulations suggests that the estimates presented here are positively biased by approximately 4%.

The estimate of the rate of increase appears to be quite robust; simulations of the response to variations in precision of abundance estimates show very little change in the resulting regression. Similarly, while the regression is strongly influenced by the 1992-1993 estimate, eliminating it results

in an estimated rate of increase of 0.046 (SE=0.0128), not significantly different than the overall estimate, though considerably less precise.

These data are insufficient to determine whether the population is continuing to grow at an exponential rate, or if the growth rate is slowing as they do not support the extra parameter for a logistic model. However, a series of high residual values in the middle years of the study period might be an indication that the rate of population change has not been constant over the 14-year period. The lowest sampling intensity occurred during these years, resulting in the lowest precision in abundance estimates and the smallest number of re-captures confounding efforts to compare these relationships.

Comparison with previous results

Previously published abundance estimates for the North Atlantic would appear to suggest a smaller abundance and a greater rate of increase than that reported here. Smith et al. (1999) published an estimate of 10,600 (9,300-12,100) for the period 1992-1993 using essentially the same data used here for that time period. Katona and Beard (1990) estimated an abundance of 5,505 (±2,617) for the period 1979-1986. The mid-point covered by their estimate is 1982-83, ten years prior to that of Smith et al (1999). The rate of increase based on these two estimates over the ten-year period is 0.0655 (annual rate 6.8%). Why do these results differ from those presented here?

While the estimate of 11,570 (95% CI 10,290-13,390) presented here does not differ significantly from the preliminary abundance estimate from these data presented by Smith et al. (1999) it is based on several methodological

improvements. As discussed above, results using variance weighting are biased by non-independence of abundance and variance estimation. The use of pooled samples here results in larger sample sizes and eliminates the bias due to variance weighting. Additionally, application of the correction to account for errors in identification improved the estimate and allowed for additional sightings to be included. Thus it provides the best estimate of abundance currently available for humpback whales in the North Atlantic.

The estimate presented by Katona and Beard (1990) is substantially lower than the estimates calculated here from largely the same data. Their estimate was calculated in such a manner that variance was accounted for twice and so is maximally influenced by the lack of independence between abundance and variance. Three estimates were calculated for each year based on different portions of the fluke represented, and the estimate with the lowest standard error was selected. The variance weighted mean was then calculated from these selected estimates. Re-calculating an estimate using data from their Table 5 but using only photographs of whole flukes and not weighting the mean yields an estimate of 7,837, more then 2,000 animals more than they estimated from the same data and comparable to the figures calculated here for the same time period.

Conclusion

These data provide the most accurate and precise estimate of abundance and change in abundance yet available for humpback whales across an ocean basin. They show growth at a rate of greater than 4% per year in the North Atlantic humpback whale population over 14 years.

It is unclear how this most recent estimate of abundance compares to pre-exploitation abundance. Early catch records are incomplete making assessment of catch history imprecise. Mitchell and Reeves (1983) estimated the abundance in the western North Atlantic prior to the greatest fishing mortality at 4,400. Catches east of about 40° W appear to have totalled about 4,500 individuals since the 1860s (Ingebrigtsen 1929; Mitchell & Reeves 1983; Sigurjónsson 1988; Thompson 1928; Tønnessen & Johnsen 1982). These figures suggest that it is possible the current abundance is comparable to historic levels, though uncertainties in estimation of pre-exploitation abundance confound any conclusion on this matter.

Figure and Tables

Table 4.1. Five estimates of abundance for 1992-1993 using different combinations of photographic quality. All estimates made using the modified estimator presented in Chapter 3, and the bootstrap variance estimator presented in Appendix B.

Photo Qualities included in estimate	N	SE	CV	Mean Square Error
1,2	10869.2	1066.91	0.0976	1138297
1,2,3+	10543.7	810.02	0.0766	656456
1,2,3+,3-	11573.4	807.68	0.0692	653051
1,2,3+,3-,L	12104.0	864.86	0.0704	749223
1,2,3+,3-,R	12033.9	840.95	0.0687	708355

Table 4.2. Estimates of abundance. All estimates are calculated by the formula in Chapter 3 to account for errors in identification with the modifications presented above. * See text for discussion of these four estimates

Years		Corrected estimates		
Feeding	Breeding	N	SE	CV%
1979-1980	1979-1980	7,260	1177	16.2
1979-1980	1980-1981	6,918	1020	14.7
1980-1981	1980-1981	8,964	1915	21.4
1980-1981	1981-1982	7,776	1529	19.7
1981-1982	1981-1982	6,944	1223	17.6
1981-1982	1982-1983	9,306	1658	17.8
1982-1983	1982-1983	8,637	1243	14.4
1982-1983	1983-1984	7,059	715	10.1
1983-1984	1983-1984	7,676	946	12.3
1983-1984	1984-1985	7,379	948	12.8
1984-1985	1984-1985	9,315	1718	18.4
1984-1985	1985-1986	10,072	2869	28.5
1985-1986	1985-1986	10,370	3257	31.4
1985-1986	1986-1987	8,147	2903	35.6
1986-1987	1986-1987	11,241	4399	39.1
1986-1987	1987-1988	9,128	3286	36.0
1987-1988	1987-1988	10,355	3269	31.6
1987-1988	1988-1989	11,207	2825	25.2
1988-1989	1988-1989	12,644	3193	25.3
*1988-1989	1989-1990	7,440	1535	20.6
*1989-1990	1989-1990	8,442	1746	20.7
*1989-1990	1990-1991	5,927	1349	22.8
*1990-1991	1990-1991	8,330	2056	24.7
1992-1993	1992-1993	11,964	793	6.6

Table 4.3. Means calculated from estimates published in Katona and Beard (1990) Table 5 using different precision based weighting methods.

	Un-weighted	**Cv weighted**	**Variance weighted**
Whole flukes only	7837	7368	5551
Whole flukes and left halves	7240	7138	5777
Whole flukes and right halves	7592	7272	5679

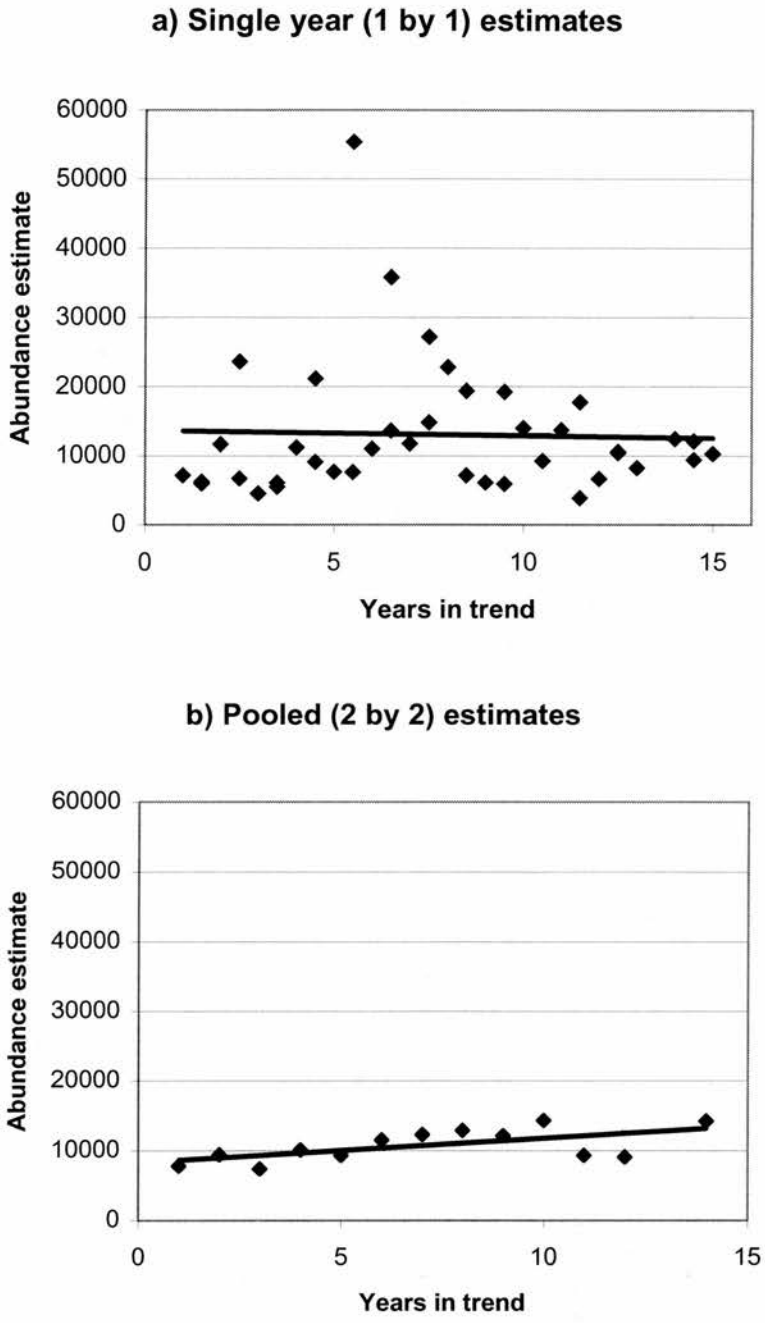

Figure 4.1. Comparison of feeding-breeding estimates when using a single year sample and when pooling years. A) estimates based upon feeding ground and breeding ground samples from a single year for the two capture intervals. B) estimates using the same data but combining the breeding ground samples from two consecutive years and the feeding ground samples from two consecutive years. Lines represent un-weighted regression. All sightings are included and no account is taken of photgraphic quality. All estimates are made with the Chapman's estimator.

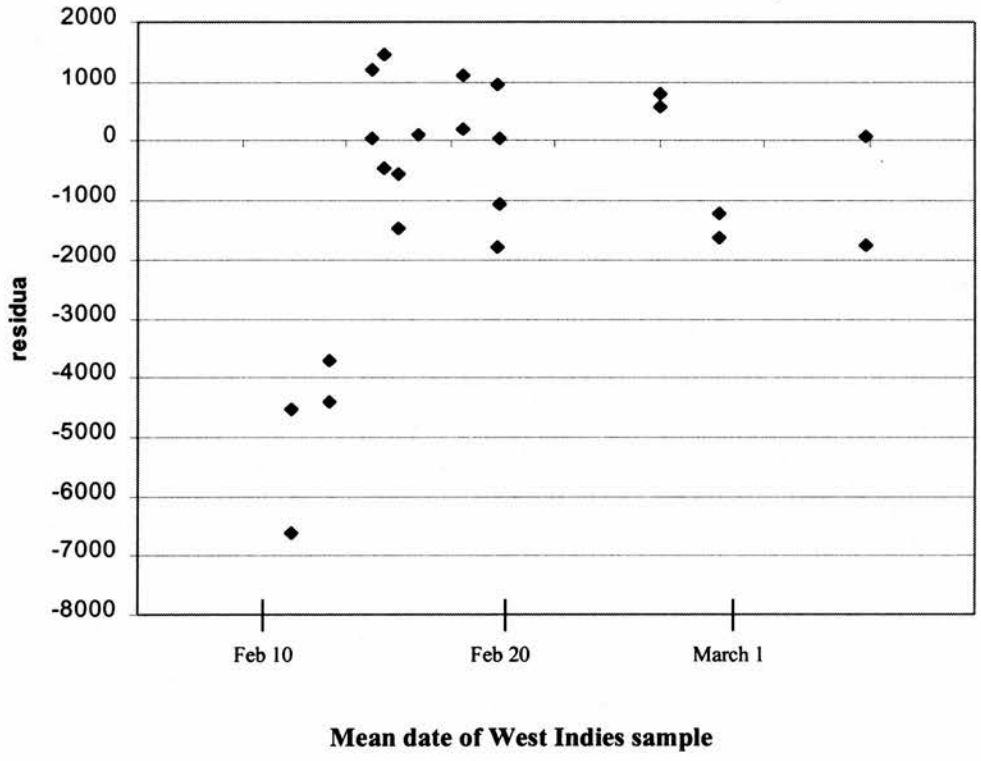

Figure 4.2. The relationship between the residual for abundance estimates (observed abundance - abundance predicted by regression) and the mean date for the West Indies sample. Note that the four estimates for which the West Indies sample is collected earliest in the season are substantially lower than expectation.

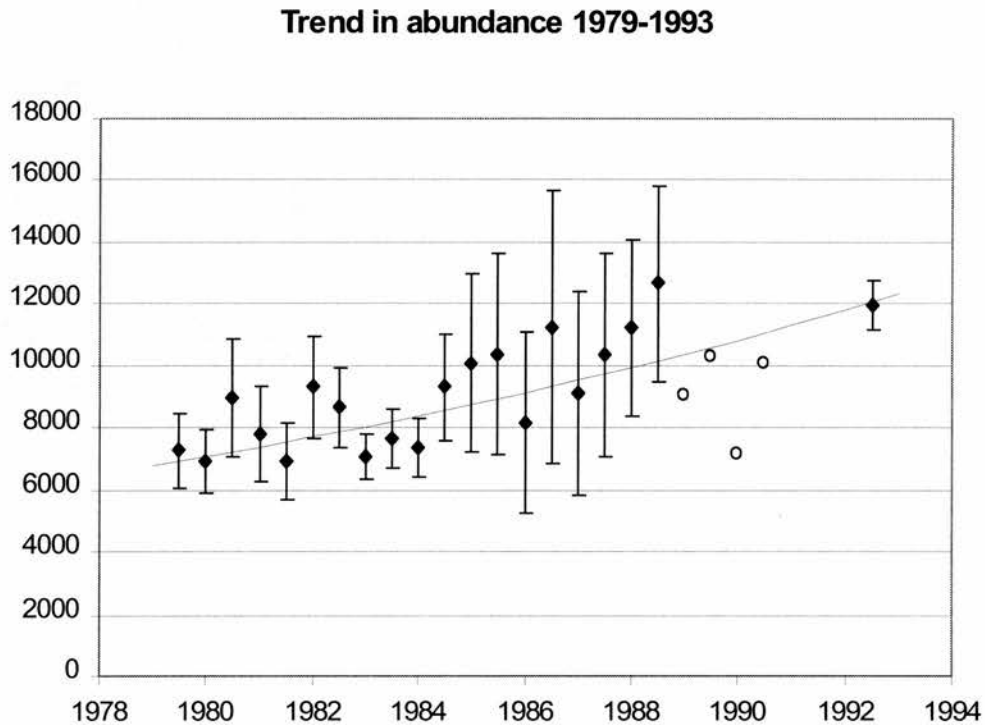

Figure 4.3. Estimates of abundance (±SE) for the North Atlantic Ocean. Open circles represent approximate corrections for estimates with known biases related to restricted dates of sampling in the West Indies. These estimates are not used in fitting the regression.

Chapter 5: Population spatial structuring on the feeding grounds

Summary

The movement patterns observed in the North Atlantic humpback whale population show complex spatial structuring on the summer feeding grounds. The existence of feeding aggregations has previously been described. However, the ocean-basin-wide nature of this study, the use of cluster analysis to delineate feeding aggregations, the use of transit distances to examine movement across a range of scales and the knowledge of the sex of a large portion of the sample, provide new insights into this phenomenon. Four geographically discrete groupings were identified using cluster analysis. Further structuring within two of these aggregations was shown. Re-sighting distances on the feeding grounds in consecutive years ranged from <1km to >2,200km. High levels of site fidelity were observed with half of all re-sightings between years at distances <40km. Thus some segregation is evident at scales of as little as tens of km, though exchange between adjacent units is high at this scale. Long distance movement occurs at a low rate; 95% of between-year re-sightings were within 550km. However, the longest observed transits demonstrate movement between feeding aggregations, leading to an exchange rate of 1.47%. Because of the over-dispersed distribution, the frequencies (F) of distances (D) observed were best modelled by an inverse allometric function ($F=6631D^{-1.24}$, $r^2=0.984$). Movement patterns reflected foraging responses to different patterns of prey availability.

More long distance movement between the US and Canada was observed in years of lower prey abundance in US waters. Significantly more long distance transits were observed in Iceland and Norway in the east both within and between years than were observed in Greenland, Canada and the US in the west. This difference appears to be related to differences in prey distribution in these areas. Sexual differences were also observed. Females moved significantly more over the longest distances than did males, but there were no differences at any other spatial scales.

Introduction

The structure of animal populations and the patterns of movement that drive them have substantial evolutionary and ecological implications. Because of the obvious implication for the breeding system and influences on gene flow, most attention has focused on the structure of breeding populations. Though less well documented, site fidelity and resulting population structuring may also be highly pronounced in non-breeding areas (Palsbøll et al. 1995; Rappole 1995; Robertson & Cooke 1999). In spite of the significance of spatial structuring and its variation across seasonal habitats, it has rarely been investigated over the entire range of a population because of logistical constraints.

Population structuring is driven by the movement patterns of individual animals. Movement allows animals to effectively utilise a patchy, unpredictable environment. Where resources are predictably associated with particular locations or features, however, survival and/or reproductive advantages may accrue to those individuals that remain in or to return to familiar areas leading to

site fidelity. Individuals may demonstrate fidelity to any point used during their lives, though to different degrees (Bollinger & Derksen 1996; Reed et al. 1998b; Robertson & Cooke 1999). Long distance migration does not imply less site fidelity; a high degree of philopatry may exist in migratory animals (Bensch 1999; but see Weatherhead & Forbes 1993). Further, movement patterns are not necessarily uniform for a species and may vary between (e.g. Mikhalev 1997; Mysterud 1999; Rappole 1995; Thouless 1995; Tyler & Øritsland 1989) or within populations (e.g. Belthoff & Gauthreaux 1991; Bollinger & Derksen 1996; Boyce 1991; Dawbin 1997), leading to additional variability in patterns of structuring.

Where site fidelity is strong, exchange between population units is limited. This population structuring has conservation implications as smaller population units are more vulnerable to localised depletion or extinction due to stochastic processes or anthropogenic effects, and are hampered in recovery from such depletion if immigration rates are low (Taylor 1997; Thomas 2000). In both ecology and conservation there is an emphasis on biological populations - interbreeding groups subject to a fairly high level of reproductive isolation from other such populations. It is clear, however, that there can be ecological differences between groups of animals within such populations. These differences may include prey specialisation and foraging behaviour (Iverson et al. 1997; Weinrich et al. 1992), migratory behaviour (Belthoff & Gauthreaux 1991; Boyce 1991) and social structure (Richards 2000). There may also be phenotypic variation between groups within populations (Allen et al. 1994) and even differences in mitochondrial genetic markers (Larsen et al. 1996; Palsbøll et

al. 1995). There is an increasing recognition, therefore, that biological populations are not always the appropriate units for conservation and management (Clapham & Hatch in press; Taylor 1997).

Humpback whales have been shown to demonstrate fidelity to both feeding and breeding areas. As large mammals with substantial energy reserves, they can travel extensively without the need for daily access to food resources. To build up and maintain these reserves they require areas of high prey density which are spatially and temporally variable and that variability is itself dynamic. It might be expected, therefore, that humpback whales would range widely across high latitude waters exploiting food resources as they become available, particularly as the marine environment is relatively free from physical barriers to such movement.

While humpback whales have the capability to forage across entire ocean basins, it appears that they do not normally do so, but rather show fidelity to specific areas of concentration known as feeding aggregations (Chapter 1). Feeding aggregations do not necessarily correspond with breeding groups. In some cases individuals from multiple feeding areas may congregate on the same breeding ground (e.g. Baker et al. 1986; Clapham et al. 1993b; Darling & McSweeney 1985; Katona & Beard 1990; Perry et al. 1990; Urbán R et al. 2000), while animals from the same feeding area may visit different breeding grounds (e.g. Baker et al. 1986; Calambokidis et al. 2000; Darling & Cerchio 1993; Darling & McSweeney 1985; Perry et al. 1990), and thus, spatial structuring of their populations may be complex.

Within the North Atlantic, humpback whales feed at sites ranging from the Gulf of Maine to the Norwegian Arctic. Five feeding aggregations were identified in the North Atlantic by Katona and Beard (1990; 1991): the Gulf of Maine, Gulf of St. Lawrence, Newfoundland/Labrador, Greenland and Iceland (Figure 1.1). In addition, humpback whales are known to occur off the coast of Norway and the adjacent waters north to Svalbard and east into the Barents Sea (Christensen et al. 1992b; Ingebrigtsen 1929). The sample of photographically identified individuals available from these eastern regions to date has been small (Katona & Beard 1991). Other data with which to assess the relationship of these individuals to those elsewhere in the North Atlantic have been limited, and interpretation of those data difficult (Mitchell & Reeves 1983).

In general, feeding aggregations have been delineated on the basis of reasonably well defined geographic areas with few animals observed in the areas between them making the distinctions intuitive. The status within Canada is, however, less clear. Katona and Beard (1990) suggested that the re-sighting patterns of individuals from the Gulf of St Lawrence warranted re-evaluation, while Whitehead and Glass (1985) demonstrated a lower rate of movement than expected between the Grand Banks and coastal Newfoundland.

While humpback whales have been intensively studied in many regions of the world, knowledge of ocean-basin-wide movement patterns has been hampered by the spatial and temporal variability in sampling effort between areas and the regional nature of many studies. I bring together the largest body of data yet available on individually identified humpback whales from across an ocean-basin to evaluate spatial structuring on the feeding grounds.

Methods

Individual animals were identified either by natural markings on the ventral surface of the flukes (Katona et al. 1979) or by molecular genetic analysis of skin biopsy samples (Palsbøll et al. 1997a). Two large collections of identification photographs exist covering the North Atlantic Ocean, the North Atlantic Humpback Whale Catalog (NAHWC) and the collection from the Years of the North Atlantic Humpback Whale project (YoNAH). In this chapter I draw upon both sources. Details of the field procedures and analytical methods used in these projects are presented in Chapter 2.

The YoNAH photographic data were the primary source used in these analyses because of the ocean-basin-wide coverage, the availability of precise location information, greater sampling intensity leading to large sample sizes and more representative sampling effort. Unless otherwise stated, analyses are based upon this sample. For some analyses I also draw upon the YoNAH genetic identifications and the NAHWC photographic sample.

Because photographic quality can influence the ability to recognise individual animals, analyses where re-sighting rates were compared were made on the basis of only good quality photographs to minimise biases related to differences in photographic quality between samples (see Chapter 2).

Gender information was obtained from genetic analysis of skin biopsy samples (Bérubé & Palsbøll 1996a; 1996b; Palsbøll et al. 1992). Where skin samples and photographs were obtained from the same sighting, genetic determination of sex is associated with the photographic identification. Where

individuals were identified as mothers with calves, but no biopsy samples were collected, such individuals were classified as females. Though reproductive behaviour may give clues to sex, this additional information was not used for samples collected during 1992 and 1993, since both males and females were identified in most other behaviour categories (Clapham et al. 1992; Robbins & Mattila 1999). Occasionally conflicting information was obtained on gender. In these instances the gender information was not used.

Prior to 1992, sex was determined on the basis of numerous factors including association with a calf, genetic determination, genital examination (Glockner 1983), and reproductive behaviour (Clapham et al. 1992; Robbins & Mattila 1999; Tyack & Whitehead 1983). Due to the uncertainty in assigning gender using reproductive behaviour, the sex designations prior to 1992 must be treated more cautiously.

Defining feeding areas

Cluster analysis was used to help define feeding aggregations. The application of cluster analysis to capture-recapture results for delineation of population units is uncommon. The technique has been used successfully to delineate management units in wildfowl using band returns (Chu et al. 1995; Pendleton & Sauer 1995), and has recently been applied to analyse geographical association patterns in North Atlantic right whales (Wade & Clapham in press). I used single linkage clustering methods to construct hierarchical cluster trees (Everitt 1974; Kaufman & Rousseeuw 1990).

Initially, the sample was divided geographically into similarly sized regions approximately 100km in diameter centred on areas of high whale density. Not all regions were contiguous; regions with few or no sightings could occur between them. Regional designations from the NAHWC were combined to represent as similar a distribution as possible, though these are not as uniform as are those used for the YoNAH results. Regional designations are illustrated in Figure 5.1. Two statistics were calculated to represent movement rates between these areas and to account for differences in sample sizes, a modification of the subset index presented by Katona and Beard (1990) and the standardised deviate (See Appendix A for details of these indices).

The cluster analysis sorted areas into groups having high rates of exchange. Since high values of both indices represented high rates of exchange, the reciprocal of the calculated values was used to construct a dissimilarity matrix for use in the clustering algorithm. All values were scaled to be greater than 0 before calculation of the reciprocal.

The method is subjective since any number of groups between 1 and the number of original units may be selected. Selection of units was based on the clustering distances and the consistency with which regions diverged with different data input. Because of the large sample size and the relatively unbiased sample, increased weight was given to results from the YoNAH photographic sample.

Distances

Great-circle distances were calculated between observed locations using the formula presented by Bowditch (1977). Distances did not account for intervening land. These provide an indication of the distance between two regions used by the animals but are not intended to represent swimming distances. Travel routes are rarely known, and individuals sighted in different years may well have migrated to the tropics between sightings.

Where there were multiple sightings of the same individual, the maximum reported distance between re-sightings was used. This under-represents site fidelity and over-estimates longer range movement. On the other hand, because effort was not random, some degree of the reverse bias will be present, with animals travelling longer distances potentially moving away from more heavily sampled regions and becoming less detectable (Koenig et al. 1996).

Results

Distances

392 individuals were identified by natural markings and 54 by genetic methods on more than one day on the feeding grounds in 1992 and 1993 and had adequate location information for both days for distance calculation to be made. This allowed calculation of 665 distances for individuals identified by natural markings and 64 re-sightings for individuals identified genetically.

There is a relationship between re-sighting distance and the difference in dates between re-sightings (correlation coefficient = 0.434, df 207, $p<0.01$,

Figure 5.2). This may indicate a tendency for animals to use the same areas at similar times during the year. Some of this effect, however, is a function of the timing of sampling effort which in many areas followed a similar pattern in the two sampling years. The shortage of re-sightings within 10km made more than 3 weeks apart reflects the tendency to sample the same areas at the same time in successive years. Similarly, if surveys follow the same course through a region in the two years it is highly unlikely that the same whale would be sampled at widely separate locations on similar dates in the two years. Indeed, restricting the data to animals re-sighted less than 1000 km apart eliminates only 3 records but reduces the correlation coefficient to 0.32. Thus time between sightings appears to be a poor explanatory variable for re-sighting distance.

Distance frequencies

The frequency of between year re-sightings (F) is greatest at distances (D) of less than 10 km, decreasing steadily and substantially with increasing distance (Figure 5.3). The median distance was only 40 km; 95% of distances were within 550 km, though a single re-sighting with a distance in excess of 2,200 km was observed.

The distribution fitted well to both the inverse allometric (inverse power) function ($F=6631D^{-1.24}$, $r^2=0.984$), and the negative exponential ($F=92.6e^{-0.013\,D}$, $r^2=0.934$, Figure 5.4). The negative exponential has been widely used to model animal movements (eg. Hjermann & Ims 1996; Olson & Van Horne 1998). This function assumes that the probability of an animal occurring at any given distance from the initial point is independent of distance (Rees 1993; Waser

1985). Thus it substantially under-represents the long distance movement observed here, predicting virtually no transit distances exceeding 400 km. The inverse allometric function is a better descriptor of overdispersed distributions, modelling more effectively both the high incidence of site fidelity and the low level persistence of movements over long distances (Baguette et al. 2000; Hill et al. 1996).

Only 7 individuals were observed to make transits longer than 1,400km, accounting for only 2.8% of the between year and 1.0% of the within year re-sightings. Four of these, accounting for all of the re-sightings separated by greater than 1,800km, resulted from movements between Iceland and Norway. The remaining three re-sightings over 1,400 km represented movements between Canada and the Gulf of Maine (n=1) and Greenland (n=2) respectively.

What feeding aggregations are there in the North Atlantic?

There were four divisions consistently apparent in the cluster results (Figure 5.5): the eastern North Atlantic (comprising Iceland and Norway), the Gulf of Maine, Greenland and Canada. Within Canada and the eastern North Atlantic further groupings were seen, but not at the same level, or with boundaries which were robust to different treatments of the data.

No individuals were identified in both the eastern and western North Atlantic. A minimum distance of 1,270km separates those whales recorded in the Denmark Strait off southwest Iceland from the nearest YoNAH sighting in Greenland. Sections of the Labrador coast are about 1,300km from the Denmark

Strait. The distance between these areas exceeds that of 95% of observed transit distances, and there are no known concentrations of humpback whales in the intervening waters; thus this lack of exchange is to be expected. Not surprisingly, with no re-sightings, the division between east and west occurred early in all treatments in cluster analysis.

Greenland

Greenland exhibited low levels of exchange with Canada. Two individuals identified as calves in Greenland during 1992 were subsequently identified in Canada in 1993, one in the Mingan Islands region and the other in the Strait of Belle Isle. Most previous re-sightings from Greenland were to the east coast of Newfoundland, though a single individual was identified in Greenland and the Gulf of Maine. Few humpback whales are found in the deep waters of the Labrador Sea between Canada and west Greenland. The closest YoNAH sightings from the two regions are separated by 1,170km. Humpbacks from Hamilton Bank off Labrador are somewhat closer to Greenland, but are still separated from it by about 900km. Thus these areas are separated by distances such that little exchange is to be expected. The separation of Greenland is apparent in the results of cluster analysis, showing early and robust divergence from other areas.

Gulf of Maine

The concentration of whales in the Gulf of Maine is relatively discrete geographically from that in Newfoundland and the Gulf of St Lawrence. Only 8 individuals have been identified on the intervening Scotian Shelf, though this

may, in part reflect low sampling effort in this region. The closest YoNAH sightings from the two areas are separated by 860km. Areas subject to intensive sampling effort are even farther apart. During the YoNAH project only a single re-sighting was made between the Gulf of Maine and Canada, an animal moving between Georges Bank and the Avalon Peninsula. Previously, individuals from several areas in the Gulf of Maine had been identified in Newfoundland, Labrador, the Gulf of St Lawrence and a single individual in Greenland. A moderately high rate of exchange has been documented between the Gulf of Maine and the northern Gulf of St Lawrence. However, there were no re-sightings between these two regions in the YoNAH results (see discussion under "movement between feeding aggregations" below).

The low re-sighting rate to other areas resulted in a clear separation of the Gulf of Maine from all other regions in cluster analysis using the YoNAH samples. However, the relatively high re-sighting rate to the Gulf of St Lawrence and to the small sample from the Scotian Shelf made this distinction less apparent in analyses using the NAHWC results.

Humpback whales in both Greenland and the Gulf of Maine are found over relatively small areas, and exchange between sub-units of these regions is high. Thus though there is evidence for structuring within them, there is no support for the division of either into more than one feeding aggregation.

Canada

The region of the Canadian coast used by humpback whales is extensive and relatively complex, with few large areas of consistently low food availability

to act as boundaries to movement of whales. Within Canada few humpbacks were identified in the southern Gulf of St Lawrence, along the west coast or the western south coast of Newfoundland. Along the east coast of Newfoundland, southern Labrador, and the Strait of Belle Isle, however, there are no identifiable gaps in distribution. Few humpback whales are known to occur over a distance of about 400km between the Mingan Islands area in the northern Gulf of St Lawrence and the mouth of the Strait of Belle Isle. The distance from the extreme locations of the Mingan Islands and the Avalon Peninsula, however, is approximately 700 km, approaching that between other feeding aggregations. Ten of the 15 individuals in the top 5% of distances reported within years, and the only ones outside the Iceland-Norway group were re-sightings within Canada. Patterns of movement within Canadian waters are presented in Table 5.1.

Cluster analysis does not support a division within Canada at the same level as separation from other aggregations, but does show considerable structuring. Major divisions within Canada consistently arise at much shorter cluster distances than those at which Canada separates from either the Gulf of Maine or Greenland, though at distances greater than divisions within either of these other regions. Further, the manner in which the region divides is variable depending on the input statistics and data set used.

The only standardised deviate in the YoNAH results which is less than –1 and two of those from the NAHWC of this magnitude represent movement between the Northern Avalon peninsula or southeast coast of Newfoundland and the Gulf of St Lawrence. Because of the lack of re-sightings between these areas

they have been treated as separate feeding aggregations in the past (Katona & Beard 1990), but the boundaries of this separation appear to be related to effort. NAHWC sampling is heavily biased toward the two extreme locations, and there is virtually no temporal overlap in sampling, with very little sampling in eastern Newfoundland between the early 1980s and the early 1990s, and almost no sampling in the Gulf of St Lawrence prior to 1982 (Figure 2.3). Given mortality and natality, this lack of temporal overlap will exaggerate any segregation between areas.

The YoNAH results taken alone suggest a north-south division at about 50° North, with the Avalon Peninsula and the Southeast coast forming a group separate from the Northern Peninsula, Strait of Belle Isle and northern Gulf of St Lawrence (Figure 5.5). This division is weak, however, with 33 individuals identified both north and south of this line and large positive standardised deviates between a number of regions on different sides of this line (Table 5.1a). It is based on a region of over 200km of coastline in which there were very few YoNAH sightings (Smith et al. 1999). This Mid-East Coast region groups in a number of ways in cluster analysis, occasionally branching earlier than any other division within Canada. This is most likely due to the small sample size from the area. Investigation of records from the NAHWC shows that humpback whales were regularly sighted in the region in previous years and there were high rates of exchange to adjacent areas to the north and south (Table 5.1b). Cluster results from the NAHWC similarly show the clearest division between the northern Gulf of St Lawrence and southeastern Newfoundland, but indicate less division along the Newfoundland coast or into Labrador than seen in the YoNAH results.

The standardised deviates of movement from the Grand Banks to other regions of Canada are consistently negative and in some cases substantially negative. The only region with a positive deviate to the Grand Banks is the Scotian Shelf, which is based upon a single re-sighting. The distance between the whale concentration on the Southeast Shoal of the Grand Banks and the nearest point of the Avalon Peninsula is almost 300 km. A reduced number of re-sightings between areas separated by this distance is to be expected and was noted by Whitehead and Glass (1985). Unfortunately, there was no offshore effort during the YoNAH project, and so it is difficult to evaluate the level of segregation between these areas beyond the analysis presented by Whitehead and Glass (1985).

Eastern North Atlantic

Whales are distributed over large areas in the eastern North Atlantic and their movements differ from those in the west. The group sampled in the Greenland Sea near Jan Mayen is only 375km from the nearest YoNAH sample from Iceland. However, between this Iceland/Jan Mayen group and the nearest sighting from the Barents Sea there is an intervening distance of over 1,200km in which only a single animal was identified. Such a discontinuity suggests that there would be little exchange between the two locations and that they would constitute separate feeding aggregations. Long distance movements between these regions both within and between years are relatively common, however. Thus cluster analysis does not support this division. The strongest and most consistent division in the area separates eastern and western Iceland, linking each with a region from Norway (Figure 5.5). Eastern Iceland has a relatively high

exchange with the Barents Sea, while there are several re-sightings between western Iceland and the Jan Mayen area.

The highest concentration of whales in the area shifts to the north and east through the summer. Humpbacks appear in numbers earliest to the south of Iceland where sampling was conducted primarily during June. Humpbacks were next photographed off Jan Mayen in late July. Photographs from the Norwegian Sea near Bear Island were collected in late July and early August, then in the waters off Hopen Island during late September. Most individuals sighted more than once either within or between seasons followed this northeasterly progression, though one individuals was observed to move 620 km almost due west over a period of just six days. The north-easterly trend must be treated cautiously, as the seasonal trend in the sampling effort similar to that of the observed movements. However, the YoNAH effort distribution was established on the basis of prior data on when numbers are highest in each area (Christensen 1977; Christensen et al. 1992b; Ingebrigtsen 1929; Martin et al. 1984a; Øien 1990; Sigurjónsson & Gunnlaugsson 1990b).

The exchange between Iceland and Norway both within and between seasons is considerably higher, and the distances between sightings substantially greater, than that observed in any other region of the North Atlantic. Indeed, within feeding area movements reported here are equivalent to the migratory distance from the Gulf of Maine to the West Indies. No between year re-sightings were identified in Norwegian waters, but 3 within year and 2 between year re-sightings were made between Norway and Iceland. The median re-sighting distance for all animals identified more than once either within or between years

in Iceland and Norway during 1992 and 1993 (eastern areas) is 148km. The corresponding median for Greenland, Canada and the Gulf of Maine (western areas) is just 25km. The distribution of re-sighting distances is significantly different between animals from the eastern areas and those from the western areas (Kolmogorov-Smirnov two sample test, p=0.012).

Movements between regions

Of 184 individuals identified on the feeding grounds in the western areas during both 1992 and 1993 from photographs of quality 3+ or better, only two were seen in more than one of these four feeding aggregations detailed above. This yields a rate of exchange between feeding aggregations in successive years of 1.09%. . An additional re-sightings was made based upon a quality 3-photograph for an overall rate of exchange of 1.35%. Individuals identified in more than one feeding area in the NAHWC are presented in Table 5.2. The majority (14 of 25) of those individuals with sightings in more than 2 years were observed to return to a previously visited region after being identified in another on at least one occasion.

The only long distance re-sightings within a year identified in the YoNAH results were three individuals photographed and one genetically identified in both Iceland and Norway. A total of 12 individuals was identified in multiple regions in the same year from the NAHWC, all re-sighted in the Gulf of Maine and Canada. All of these occurred between 1983 and 1989 with the highest incidence in 1984 and 1988. The interval between these sightings ranged from 14 to 143 days.

Gender and age differences

Differences between males and females were examined in the western region only (Figure 5.6) since the sample size of known sex individuals in the east was not adequate for analysis. The distribution of distances was very similar between sexes over most spatial scales (Kolmogorov-Smirnov two sample test, $p=0.781$), though the distributions diverged significantly at distances greater than 400 km (Kolmogorov-Smirnov two sample test, $p=0.031$). Females were observed to exhibit more long distance movement in several collections (Table 5.4), however these sample sizes are small limiting the power of the tests, and the results did not differ significantly from the ratio of known genders in the collections from which they were taken. Anecdotally, the sole individual to be identified in the Gulf of Maine, Canada and Greenland was seen with a calf during the 1989 season and is presumed to be an adult female.

Minimum age estimates (see Stevick 1999) for individuals which were sighted in more than one feeding area ranged from 2–18yr. Five of the individuals that moved between areas (2 from YoNAH, 3 from the NAHWC) were calves when first identified, and were sighted in different areas in their second or third summers.

Discussion

What is a feeding aggregation?

These results demonstrate neither random mixing of individuals within feeding aggregations nor lack of movement between them. Rather, they show

varying levels of structuring on the feeding grounds; the pattern of re-sighting illustrated here indicates that the extent of movement between two areas is a function of the distance between them (Figure 5.7). The very low rate of movement over even modest distances is striking in an animal capable of such long distance travel.

Different levels and types of spatial structuring are evident in this population depending on the spatial scale at which the population is observed (Kotliar & Wiens 1990; Thomas & Kunin 1999). The distribution of animals is linked in a scale dependent manner to patterns of distributions of their principal food and its scale of predictability (Biggs et al. 2000; Fauchald et al. 2000; Fragoso 1999; Reid et al. 2000; Whitehead 1996). Humpback whales in the North Atlantic exploit principally schooling fish and secondarily euphausiids (Chapter 1). Both of these prey are often associated with oceanographic features and bottom topography which demonstrate variability over tens of km. At scales of about 100 km, with habitat units of 10 km or so, therefore, individuals appear to be highly mobile with frequent movement in and out of habitat patches. At scales of several hundreds of km, some structuring will become evident, with high degrees of site fidelity to specific habitat patches, but still with a substantial amount of movement between these areas. At scales of several thousands of kilometres, and spatial units of 100s of km, individuals show low mobility. The predictability of prey resources within single habitat units is likely to be high and so there will be little or no incentive for movement between spatial units. Regions of low whale density which extend over more than a few hundred kilometres will appear to separate discrete population units. In areas without

discontinuities in distribution or sampling, population divisions may not be as clearly defined, yet movement between remote locations will be low.

Little previous attention has been given to this sub-regional preference within feeding aggregations. Recently, however, a higher rate of re-sighting has been shown to occur within the southern and northern sectors of the sampling range in Greenland than between these areas, and this difference has been shown to persist over multiple years (Larsen & Hammond 2000). Similarly, persistent preference to specific high-use habitats has been demonstrated in the Gulf of Maine (Stevick et al. 1993, J. Robbins, pers comm).

Route segregation

If individuals have preferential routes that they follow through an area this may further help to explain the observed pattern of exchange. High fidelity rates to migratory staging areas have been shown in many birds (Kaiser 1999; Reed et al. 1998a; 1998b; Schwartz & Ganter 1995) and also in some mammals (Boyce 1991), suggesting that they have preferences for migratory routes. While such preferred routes have not been suggested in humpback whales before, they are a logical outgrowth of feeding site fidelity. Feeding area philopatry is determined through familiarity with sites frequented by a calf when travelling with its mother during its first year (Clapham 1993; Clapham et al. 1993a; Palsbøll et al. 1995; Weinrich 1998). The routes followed to and between these areas are equally likely to be learned through maternal association.

The existence of preferred routes of travel could help to explain, for example, the low rates of exchange between animals to the east and west of

Newfoundland but their mutual presence along the south coast of Newfoundland and in southern Labrador. Individuals arriving in spring to the south of Newfoundland may travel west into the Gulf of St Lawrence toward feeding areas along the Quebec shore, Strait of Belle Isle or beyond to the Northern Peninsula or Labrador. Alternatively, they may head east to feeding areas along the Avalon Peninsula and the east coast of Newfoundland, or beyond to the Northern Peninsula, Strait of Belle Isle or Labrador. Such a pattern would help to explain the comparatively low re-sighting rate between the northern Gulf of St Lawrence and the Northern Peninsula and the high rate of movements from each to the Strait of Belle Isle.

This indicates that spatial structuring may not be completely represented by geographically discrete groups of individuals. Such semi-geographical structuring, in which groups of individuals demonstrating very different patterns of movement utilise common areas, was shown to occur in northern right whales by Wade and Clapham (in press) using cluster analysis. Few areas in the North Atlantic have adequate sampling intensity for humpback whales to support the type of cluster algorithm used in their analysis, however.

Thus feeding aggregations are the result of the fidelity of individual animals to specific feeding sites and potentially also to travel routes, coupled with discontinuities in distribution. The primary factor separating feeding aggregations is likely to be discontinuities in availability of feeding habitat. The limited amount of movement across regions of poor habitat may be exacerbated by the costs associated with that movement. In addition to the energetic requirements of any long distance travel, movement across large tracts of poor

habitat also carries a cost in lost feeding opportunities which may reduce the likelihood that an individual will undertake such travel unless the probability of payoff is predictably high.

North Atlantic feeding aggregations

Four aggregations appear clearly from these data. However, it is possible that the strength of some of these divisions may be in part artefacts of sampling effort (Koenig et al. 1996; Thomas & Kunin 1999). For example, while there have only been a small number of humpback whales identified on the Scotian Shelf between the Gulf of Maine and Canada, humpback whales have been sighted in the region (Kenney 1994) and recent sighting surveys have reported substantial numbers during summer (Clapham 1998; Clapham & Cole 1999). This may reflect a lack of prior effort in the area or it may be linked to the influx of capelin into the Scotian Shelf since the mid-1980s, an area in which it was previously all but unknown (DFO 1997), as these recent sightings of humpback whales are concentrated in the areas of the shelf with the highest capelin densities (Clapham 1998; Clapham & Cole 1999; DFO 1997).

Of the eight individuals identified on the Scotian Shelf, one was also identified in the Gulf of Maine and two in Newfoundland with sightings on the Grand Banks, the Avalon Peninsula and the mid-east coast. This suggests that while Newfoundland and the Gulf of Maine may have little exchange of animals, there may be intervening habitat with high levels of exchange to both, complicating delineation of the boundary between these aggregations. Similar situations may exist between other aggregations as well.

Status of feeding aggregations in Canada

Because the habitat used by humpback whales in eastern Canada covers a broad area, the degree of separation between some locations, when considered in isolation, is very high. This segregation does not appear to be comparable to that between different feeding aggregations, however, and there are intervening areas with high rates of exchange to both areas. If individuals show preferred routes of travel, this would further limit exchange of individuals between (for example) the southern east coast of Newfoundland and the northern Gulf of St Lawrence. Thus considerable structuring of the population exists within Canada, but there are no unambiguous divisions within it, and exchange rates across any delimited boundary will be high. Cluster analysis does not support the division of Canada at the level of other feeding aggregations. These complexities suggest that for most applications eastern Canada is most appropriately treated as a single, though complex and geographically stratified, feeding aggregation. However, the high degree of segregation between animals using some areas may make separate treatment appropriate for some management purposes.

Status of feeding aggregations in the eastern North Atlantic

The pattern of movement demonstrated in and between Iceland and Norway is different to that observed elsewhere in the North Atlantic, with individuals travelling long distances over short periods of time as a matter of routine. This may indicate that individuals in the region show less site fidelity and are less apt to return to specific locations than has been documented in humpbacks elsewhere. While the sample is small, the existence of re-sightings

over short distances between years in Iceland suggests that this is probably not the case. The pattern could alternatively reflect site fidelity to regions of abundant, seasonally predictable food supplies as elsewhere, but longer distance movements between such sites reflecting the scale of resource predictability in the region.

Movements of individual whales between Iceland and Norway, and within and between the Barents and Norwegian Seas and the Denmark Strait have not previously been investigated. Abundance patterns from sighting surveys and catch records, however, indicate a seasonal progression through the region. Sighting surveys show the regions of greatest humpback whale density to move progressively north and east (Christensen et al. 1992b; Martin et al. 1984a; Øien 1990). Sigurjónsson and Gunnlaugsson (1990b) show that humpback whales in the Denmark Strait off south western Iceland are most abundant in June and early July, with lower numbers in most areas after July 15. The animals seen late in the season are more common to the north of the primary early season distribution. They further theorise that in some years large numbers of humpbacks may have left the region before the sighting effort intensifies in early July. A similar seasonal progression has been noted off Norway. Sighting surveys, catch figures and opportunistic sighting reports show humpbacks in May and June primarily in coastal waters of northern Norway. The distribution shifts offshore to the eastern Norwegian Sea and off Bear Island in late June and July moving progressively north and east, with most sightings in the Barents Sea off Hopen Island by September and October (Christensen et al. 1992b; Ingebrigtsen 1929).

These observations suggest that humpback whales are responding to abundant but transitory food resources in the region. While a comprehensive evaluation of prey availability has not been possible, the trend is consistent with the general distribution pattern of principal prey items off Iceland and in the Barent's Sea.

Euphausiids are a common prey of humpback whales in many parts of the world (Chapter 1). In the Norwegian Sea, *Thysanoessa inernis* is abundant, and has been reported as a principal prey of humpback and blue whales over the shelf in spring and early summer (Hjort & Ruud 1929). Ingebrigtsen (1929) reports that 'krill' were the principal prey of humpbacks caught off Bear Island from late June through August. There are few data on stomach contents of humpback whales caught in Iceland, but *Meganyctiphanes norvegica* are the primary prey of fin whales caught to the south and west of Iceland (Vikingsson 1998). The proportion of fin whales caught with empty stomachs increases progressively from July through September, suggesting that euphausiid concentrations decline in the region through the summer (Vikingsson 1998). There is a highly significant negative correlation between the number of humpback whales sighted per unit of effort by Icelandic whaling vessels (Sigurjónsson & Vikingsson 1998), and the proportion of fin whales caught with empty stomachs (Vikingsson 1998) in the same area (correlation coefficient –0.754, $p<0.01$). Eliminating sightings from late May, when humpbacks may still be migrating into the region improves the correlation (correlation coefficient –0.877, $p<0.001$).

Capelin are also reported to be a major prey item in the eastern North Atlantic (Christensen et al. 1992a; Ingebrigtsen 1929). There are two stocks of

capelin in the region, one to the north and west of Iceland and the other in the Barents Sea (Gjøsæter 1998; Vilhjálmsson 1994). The distribution of capelin in these waters is highly unpredictable over small temporal and spatial scales (G. Vikingsson, pers. comm.). At larger scales, however, both stocks are associated with meso-scale oceanographic features. The Icelandic stock is broadly associated with the Polar Front, the boundary between the cold southerly current along the east coast of Greenland and the warm water current moving north through the Denmark Strait. This boundary is highly dynamic, but generally extends from the Denmark Strait east and north in the waters between Iceland and Jan Mayen. The Icelandic stock spawns in March to the southwest of Iceland, moving north and east through the summer in association with this current boundary (Vilhjálmsson 1994). The Barents Sea stock spawns in coastal waters of northern Norway in March and April, moving north into the Barents Sea to feed in summer and autumn. Their distribution is associated with meso-scale features related to warm water intrusions into the Barents Sea and the resulting boundary of the ice (Gjøsæter 1998). Substantial year to year variation in abundance and distribution in both regions has been correlated with variation in sea temperature reflecting changes in these larger scale features (Astthorsson & Gislason 1998; Gjøsæter 1998).

This larger scale predictability may result in predictable seasonal shifts in abundance. The lack of temporal and spatial predictability of prey on smaller scales is consistent with greater short term mobility of predators. It suggests that humpback whales congregate to the south of Iceland, off coastal Norway and along the shelf break west of Bear Island early in the season to take advantage of

euphausiid concentrations, progressing to the north following capelin later in the summer and autumn as the euphausiids decline in abundance. This pattern is also consistent with the division of re-sightings within the eastern North Atlantic; with those whales to the west of Iceland in early summer following the Icelandic capelin stock north along the Polar Front, and those to the east more likely to move to the Barents Sea.

Shifts by humpback whales due to unpredictable changes in food availability have been reported from other regions and within Norwegian waters (see below). Thus it is even possible, though it appears unlikely, that the pattern reported here is anomalous and related to a perturbation in food availability during 1992 and 1993.

The movement data unambiguously show a difference in movement patterns between the eastern and western North Atlantic. They suggest that humpback whales from the Denmark Strait east may even constitute a single feeding aggregation, albeit an atypical one in many respects. The existence of genetic differences between individuals sampled off Iceland and Norway (Larsen et al. 1996), however, suggests considerable discreteness between these areas which is not evident in the movement results. The data are few and the area large, however, and so further work in this region will be required to clarify the status. In particular, broader geographic coverage with more effort late in the season off Iceland and early in the season in the Barents Sea is needed. Analysis of the genetic sample from Iceland on a finer geographic scale may also confirm or refute the east-west segregation suggested by cluster analysis.

Movements between feeding aggregations

Animals must forage on a scale over which resources are predictably available (Fauchald et al. 2000; Jaquet & Whitehead 1996; 1999; Reid et al. 2000; Whitehead 1996). While schooling fishes are often predictably associated with oceanographic features, which would support high site fidelity, they are also notoriously unpredictable in abundance (Smith 1994). This lack of predictability may lead individual whales to make occasional long distance movements that may take them across feeding aggregations or even from one feeding aggregation to another. While such forays need not be the result of immediate food shortages, and may simply be exploratory, they may well occur more frequently during periods of changing food supplies.

Chittleborough (1959; 1965) reported a year with anomalous movement in Australia and associated it with shifts in prey abundance in the Antarctic. Changes in humpback whale abundance and distribution within regions in the North Atlantic have also been correlated with changes in prey abundance (Christensen et al. 1992b; Payne et al. 1986; 1990; Piatt et al. 1989; Weinrich et al. 1997; Whitehead & Carscadden 1985). The higher incidence of movement between the Gulf of Maine and Canada between 1983 and 1989 could be in response to alteration in food availability.

In order to examine this I investigated indices of humpback whale movement and of potential prey abundance in both the US and Canada. I calculated the rates of movement for animals sighted in the US and Canada within a single year and in adjacent years. These indices show low levels of movement through 1982, a marked increase beginning in 1983 and a fairly high

level until 1989, then steadily declining rates of exchange through 1993 despite increased sampling effort (Figure 5.8). Comparison was also made to Newfoundland and the Gulf of St Lawrence separately. However, as this showed no major differences in pattern and low sampling intensity in some years increased the variability, this separate comparison was not used in the analysis.

Two indices of prey abundance are available for the Gulf of Maine. The abundance of sand lance in the inshore southern Gulf of Maine is represented by the mean number caught per standard tow (log transformed) during spring groundfish surveys in stratum 26. The combined abundance of herring and mackerel in the entire Gulf of Maine and Georges Bank are represented by the weight per standard tow of a complex of species, termed the principal pelagics index, largely comprised of herring and mackerel. These data were obtained from the United States National Marine Fisheries Service (Northeast Fisheries Science Center, Woods Hole, Massachusetts, USA). An index of relative year class strength is available for capelin in Newfoundland and Labrador (SA2 + division 3KL)(Carscadden et al. in press; DFO 2000). This was extrapolated to give relative year class strength of 2 and 3 year old capelin for each year. The relative strength of this age class has been shown to be correlated with the nearshore abundance of humpback whales off Newfoundland (Whitehead & Carscadden 1985). Unfortunately, no index of capelin abundance is available for the Gulf of St Lawrence prior to 1990 (DFO 1999, J. L. Beaulieau, pers comm). In addition, catches of capelin in spring and autumn surveys off the Scotian Shelf were considered (DFO 1997).

There is a weak negative correlation between humpback whale movement and indices of sand lance abundance in the southern GOM. The correlation is significant when whale movement is compared with fish distribution the preceding year. This same lag is observed between herring abundance and movement, though the relationship is weaker and is not significant. The relationship between movement and abundance of Scotian Shelf capelin is also significant, but did not demonstrate a time lag (Table 5.3).

These relationships suggest that a low abundance of two principal prey simultaneously in the Gulf of Maine in the mid-1980s led to more individuals travelling long distances for foraging. The period of greatest movement coincides with a prolonged period of low sand lance abundance.

The weakness of the overall correlation reflects the low rate of movement during other periods of low sand eel abundance. A total absence of sand lance during 1990, 1991 and 1993 did not result in similar observed movement of humpback whales. Indeed, the movement index dropped steadily through 1993. During the 1990s, however, herring and mackerel abundance was high within the Gulf of Maine, so an alternative prey resource was available locally. This suggests that humpback whales made a shift from sand lance to herring (Weinrich et al. 1997) or perhaps mackerel within the Gulf of Maine at this time rather than leaving the Gulf of Maine to go elsewhere. The sand lance and principal pelagics indices are on similar scales, and combining them yields a rough indication of overall prey abundance for the Gulf of Maine. The relationship between movement and this combined index is stronger than with

either prey index independently (correlation coefficient –0.391, $p<0.01$, Figure 5.9).

The sudden increase in capelin on the Scotian Shelf beginning in the late 1980s corresponds to the decline in observed movement between the US and Canada. However, because this increase occurred at the same time as the herring increases in the Gulf of Maine (correlation coefficient 0.83, $p<0.01$), the relationship with whale movement may be artefactual. On the other hand, whales moving out of the Gulf of Maine during the sand lance declines in the 1990s may have found adequate food on the Scotian Shelf, while there may have been little to interest them there during the 1980s, leading to fewer animals observed travelling to Newfoundland or the Gulf of St Lawrence during the later period.

Thus, though whales utilise prey for which abundance data are not available and the spatial relationship between whales and their prey is more complex than reflected here, movement of humpback whales between the US and Canada is related to a period of relative scarcity of schooling fish in US waters.

Oceanographic conditions are known to influence abundance and distribution of prey (eg Carscadden et al. in press; Leggett et al. 1984). There is no clear pattern in oceanographic conditions between 1978 and 1983 as reflected in the North Atlantic Oscillation (www.cda.noaa.cov/ENSO/enso.mei_index). There were, however, strong El Niño events that ended in 1983 and 1987 (www.cpc.ncep.noaa.gov/data/teledoc/nao) the years prior to the greatest movement, and the ENSO phenomenon is known to have global ramifications, so

some correlation of prey with large-scale oceanographic phenomena is not out of the question.

Rates and extent

The excellent fit of the observed movement pattern to the inverse allometric function graphically demonstrates the over dispersed distribution, with both very high fidelity to small areas and occasional long distance travel (Figure 5.4). Given the swimming capabilities of humpback whales, the infrequent nature of long distance travel observed in most areas is striking. Individuals consistently return to within a few km of the same location after intervening migrations of thousands of km. Once on the feeding grounds, the limited movements seen are also surprising. Sustained speeds of over 5 km/hr have been reported for humpback whales (Dawbin 1966; Mate et al. 1998), which would allow a humpback whale to swim 575km, a distance greater than 95% of the distances observed, in less than five days.

Humpback whales are known to interrupt migration to feed if adequate resources are available (Best et al. 1995). Thus it is possible that individuals bound for one feeding area may be sighted in another while making a temporary stop on migration. Indeed, a higher rate of re-sighting between feeding aggregations might be expected from an examination of the likely migratory routes of humpback whales in the North Atlantic. Whales bound from the West Indies to west Greenland by the shortest, great circle route, would have to pass through the Strait of Belle Isle or around the Avalon Peninsula of Newfoundland, while those headed to Iceland or Norway would pass near the Avalon Peninsula

or over the Grand Banks. Further, asymmetric migration is common in some bird groups where routes are associated with prevailing weather patterns (Rappole 1995). Acoustic tracking of humpback whales off Britain showed an offshore southerly migration in the autumn and winter, but failed to identify a northward migration in spring (Charif et al. in press), perhaps indicating that individuals are following a track farther to the east when travelling north. Thus a migration pattern following the North Atlantic gyre is possible.

While the YoNAH sampling effort specifically avoided early and late season sampling, support for this migratory stopover theory may be found in earlier years. Of 13 instances in which the same individual was identified on different feeding grounds in the same year (12 individuals), 11 were seen in the area nearest to the West Indies earlier in the season.

Age and sex differences

These data indicate that there may be a greater tendency for long distance movement on the feeding grounds among females. Females are over-represented among animals moving between feeding aggregations, and are disproportionately represented among the individuals moving the longest distances. The sample of animals travelling long distances is small, however, and most differences are not significant.

Long distance travel in many mammals is associated with males; longer distance movement by females is unusual (Dingle 1996; Greenwood 1980). There are some indications that male humpback whales are more likely than females to move between breeding grounds (Darling & Cerchio 1993; Palumbi &

Baker 1994; Salden et al. 1999). While greater movement on the breeding grounds by males is probably related to reproductive strategies (Greenwood 1980), greater movement by females on the feeding ground may be a function of greater energetic demands relating to body size or to reproduction (Belthoff & Gauthreaux 1991; Lockyer 1981).

The sample of individuals of known age is too small to quantitatively evaluate, and minimum age estimates may severely underestimate age. However, there is no clear bias. Minimum age estimates span nearly the entire range possible given the duration of the study and show no clear pattern.

Influence on abundance estimation

Movement between feeding areas results in the violation of the assumption of closed populations in capture-recapture estimates of population parameters for feeding areas. If not taken into account, this will lead to artificial inflation of abundance estimates and depression of survival rates since it will make some individuals unavailable for re-capture.

Because immigrants to a feeding area will not have been sighted there during the initial sample, they are all unmarked. The movement of unmarked individuals into the population and of potentially marked individuals out of it artificially diminishes the proportion of marked individuals in the second sample. A modification of the Petersen two-sample estimator can account for this bias.

Let:

N = abundance

n_i = number of individuals identified in sample *i*

m_2 = number of individuals identified in both samples

e = rate of exchange

Then:

n_1 = individuals marked at time 1

$n_1(1\text{-}e)$ = number of marked individuals in the population at the time of sample 2

So:

$(n_1(1\text{-}e))/N$ = proportion of marked individuals in the population at the time of sample 2

The modified Petersen two sample abundance estimator is, therefore:

$$\hat{N} = \frac{n_1(1-e)n_2}{m_2}.$$

So movement results in a positive bias in abundance estimation equivalent to the rate of exchange. The rate of movement between feeding areas shown here will result in abundance estimates for feeding areas in the western North Atlantic which are positively biased by between 1.1 and 1.4% if this effect is not taken into consideration. Since there were no re-sightings observed between the eastern and western North Atlantic, and movements in the east are different than those in the west, this correction cannot be applied to the eastern region.

Many individuals which move between feeding areas subsequently return to the region in which they were first sighted. Such temporary emigration may result in substantial biases in the use of open population models (Pollock et al. 1990). Whitehead (1990) developed a model to estimate and account for temporary emigration in multiple re-capture experiments for closed populations. Calculation of the likelihood function is, however, impractical for large data sets such as this (Whitehead 1990), while the heterogeneity in these data causes problems in multiple recapture models (Pollock et al. 1990).

In addition to the problem of movement between areas, abundance estimates in feeding areas have been shown to be severely negatively biased by patterns of site fidelity within them (Hammond 1990; Hammond et al. 1990b). Thus unbiased estimates of abundance for feeding areas will be difficult to obtain without considerable attention to movement patterns both within and between the regions sampled.

Conclusion

Within the North Atlantic, humpback whales demonstrate high levels of persistent site fidelity on the feeding range. This leads to geographically discrete feeding aggregations. The ocean-basin-wide nature of this study, the use of movement patterns to delineate these aggregations, the calculation of transit distances for examination of movement across a range of scales and knowledge of the sex of a large portion of the sample, provide new insights into this phenomenon.

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Tables and Figures

Table 5.1. Pattern of re-sightings within eastern Canada. Each cell contains standardised deviate (number of resightings). Standardised deviates >1 light shading, <-1 dark shading. Note that many deviates are negative even between regions in close proximity to one another. Since this represents less movement than expected given random movement through the entire population, this indicates high levels of site fidelity over small scales. A) results from YoNAH project.

Region (n=)	SN	SA	NA	SE	ME	NP	SB
South Newfoundland (4)							
South Avalon (83)	-0.17 (0)						
North Avalon (268)	-0.30 (0)	11.60 (18)					
South East Coast (148)	-0.23 (0)	2.85 (4)	14.35 (30)				
Mid East Coast (2)	-0.03 (0)	-0.12 (0)	-0.22 (0)	-0.16 (0)			
North Peninsula (124)	-0.21 (0)	0.12 (1)	1.85 (6)	2.71 (5)	6.68 (1)		
Strait of Belle Isle (407)	-0.39 (0)	0.63 (4)	0.19 (10)	2.54 (11)	3.50 (1)	14.19 (34)	
Northern Gulf of St Lawrence (52)	-0.13 (0)	-0.61 (0)	-1.10 (0)	1.64 (2)	-0.09 (0)	1.93 (2)	17.13 (25)

B) results from NAHWC.

Region (n=)	SS	GB	SN	SA	NA	SE	ME	NP	BI	QG	SL
Scotian Shelf (8)											
Grand Banks (262)	1.92 (1)										
South Newfoundland (30)	-0.14 (0)	-0.82 (0)									
South Avalon (146)	-0.32 (0)	-0.72 (2)	-0.62 (0)								
North Avalon (562)	0.98 (1)	-0.76 (10)	-0.38 (1)	5.60 (22)							
South East Coast (471)	-0.57 (0)	-0.51 (9)	-1.11 (0)	11.10 (33)	15.71 (98)						
Mid East Coast (79)	4.04 (1)	-1.34 (0)	-0.45 (0)	3.01 (4)	3.66 (11)	5.46 (13)					
Northern Peninsula (29)	-0.14 (0)	-0.81 (0)	-0.27 (0)	-0.60 (0)	3.87 (6)	4.44 (6)	6.30 (3)				
Strait of Belle Isle (152)	-0.32 (0)	-1.86 (0)	-0.63 (0)	0.78 (3)	0.96 (10)	-0.08 (6)	-0.04 (1)	7.48 (5)			
Northern GSL (85)	-0.24 (0)	-0.67 (1)	3.79 (2)	-0.07 (1)	-1.05 (2)	-1.86 (0)	0.55 (1)	-0.46 (0)	8.41 (10)		
South Labrador (264)	-0.43 (0)	-2.04 (1)	-0.83 (0)	-0.18 (3)	1.45 (18)	4.35 (25)	0.15 (2)	4.10 (4)	0.82 (5)	-0.67 (1)	
North Labrador (21)	-0.12 (0)	-0.69 (0)	-0.23 (0)	-0.51 (0)	0.97 (2)	1.24 (2)	2.26 (1)	-0.23 (0)	-0.53 (0)	-0.39 (0)	2.20 (2)

Table 5.2. Movements between feeding areas from the North Atlantic Humpback Whale Catalog (left), and the YoNAH project (right).

Region	Gulf of Maine		Canada		Greenland		Iceland	
Canada	25	1						
Greenland	1	0	13	2				
Iceland	0	0	0	0	0	0		
East of Iceland	0	0	0	0	0	0	0	5

Table 5.3. Correlation between the standardised deviate for movement of whales between the US and Canada and various indices of abundance for potential prey. The time lagged relationship is between movement and the prey index from the preceding year.

Fish	Correlation coefficient	Lagged one year
GOM sand lance	-0.008 ns	-0.333 *
GOM herring/mackerel	-0.144 ns	-0.185 ns
Newfoundland capelin	0.050 ns	0.035 ns
Scotian Shelf capelin	-0.371 *	-0.304 ns

Table 5.4. Comparison of distances travelled by males and females. Observations in Iceland and Norway are excluded because of differences between regions. * No contingency tests were conducted in this case because of the small sample sizes.

	Natural Markings			Genetic tagging		
	Males	**Females**		**Males**	**Females**	
Median between year distance, 1992-1993	96 km (n=46)	168 km (n=44)	U=1131 p=0.377	158 km (n=13)	106 km (n=7)	U=49 p=1.00
95th percentile of between year distances, 1992-1993	547 km	789 km		547 km	585 km	
Number of individuals with re-sighting distances >500 km, 1992-1993	4	8	Chi-sq=1.76 P=0.185	2	1	*
Number of individuals identified in more than one feeding aggregation, 1978-1991	2	11	Fisher exact test p=0.148	NA	NA	

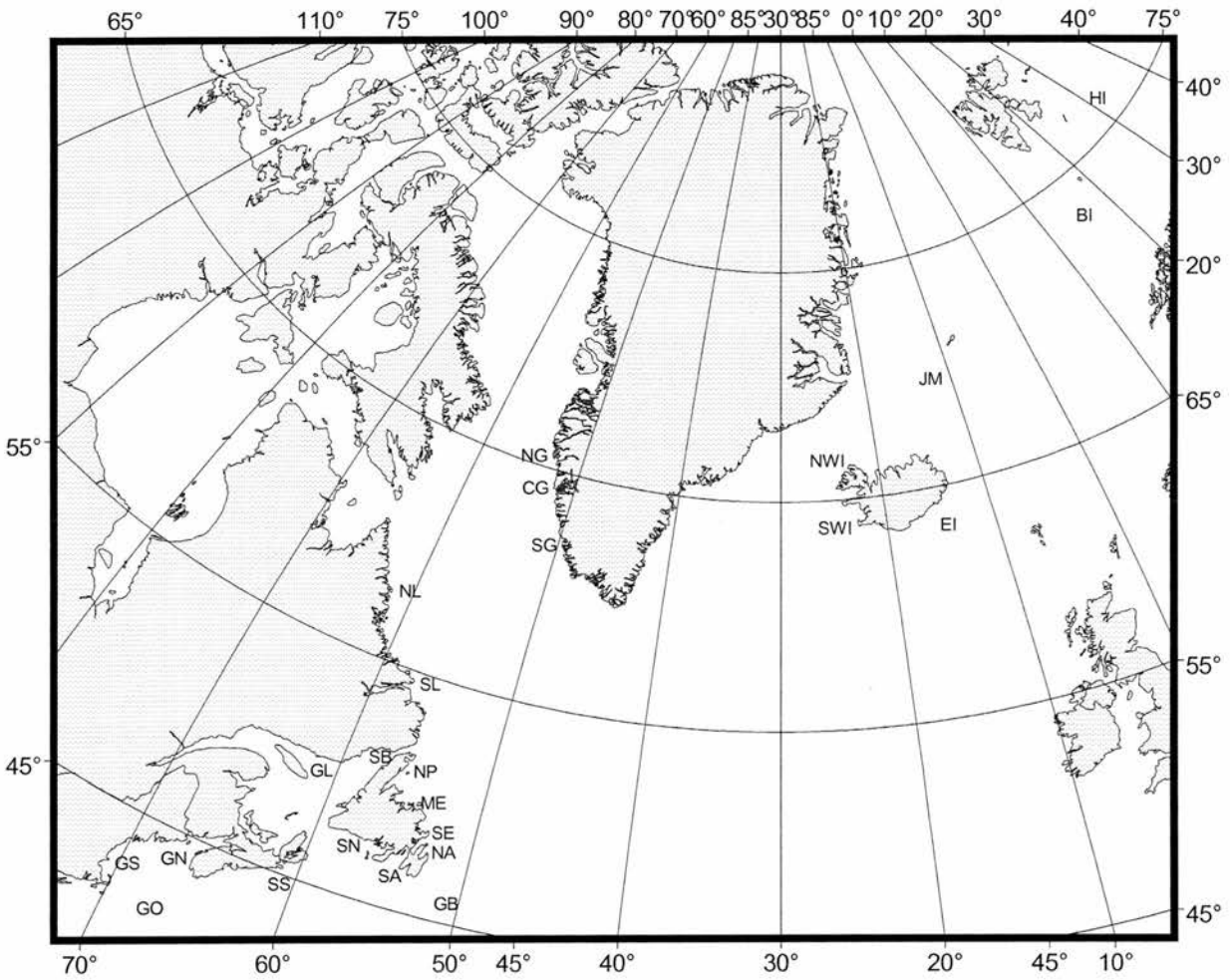

Figure 5.1. Approximate locations of the regional designations used in these analyses.

GS - Southern Gulf of Maine
GN - Northern Gulf of Maine
GO - Offshore Gulf of Maine
SS - Scotian Shelf
GB - Grand Banks
SN - South Coast of Newfoundland
SA - Southern Avalon Peninsula
NA - Northern Avalon Peninsula
SE - Southeast Coast of Newfoundland
ME - Mid-east Coast of Newfoundland
NP - Northern Peninsula of Newfoundland
SB - Strait of Belle Isle

GL - Gulf of St Lawrence, Mingan Islands
SL - Southern Labrador
NL - Northern Labrador
SG - Southern Greenland
CG - Central Greenland
NG - Northern Greenland
SWI - Southwest Iceland
NWI - Northwest Iceland
EI - East Iceland
JM - Jan Mayen
BI - Bear Island
HI - Hopen Island, Barents Sea

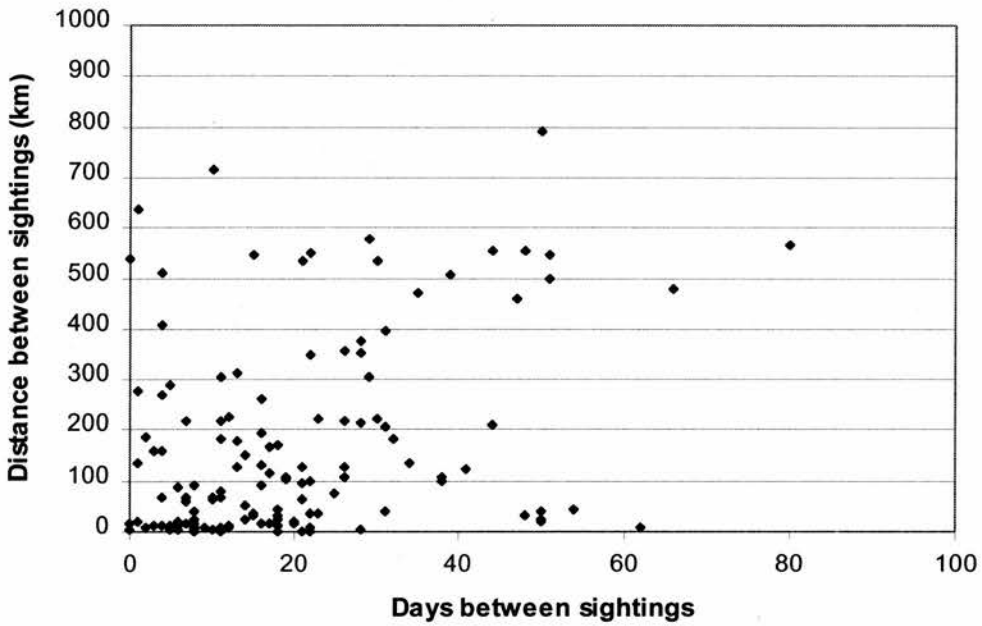

Figure 5.2. The difference in sighting dates of individuals sighted in the feeding grounds in both 1992 and 1993 related to re-sighting distance. Distances greater than 1000km are not shown.

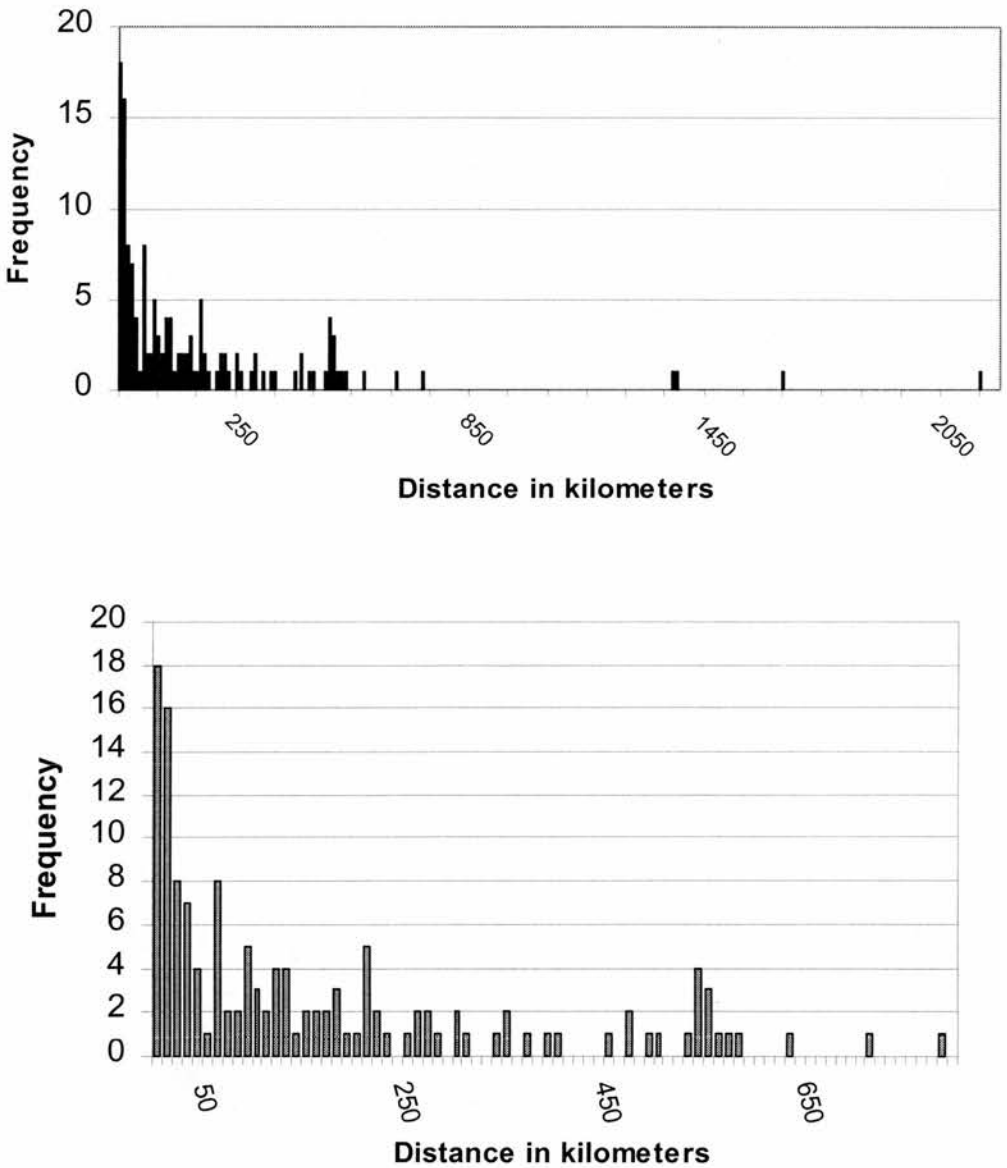

Figure 5.3. Frequency of observed re-sighting distances between years. Only the maximum distance reported for each individual is shown. Top- all distances. Bottom- only distances less than 800 km. The presence of several concentrations of animals in Canada separated by about 550km leads to a slight peak in re-sightings at this distance.

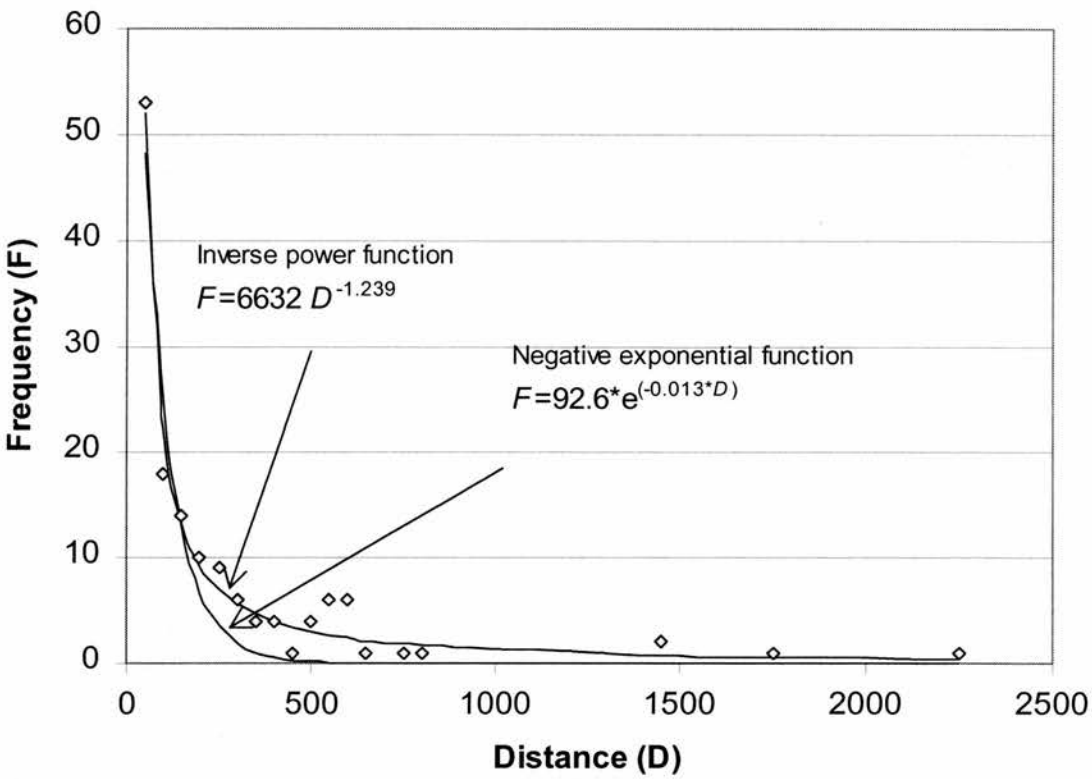

Figure 5.4. Negative exponential and inverse allometric functions fit to the frequency distribution of observed re-sighting distances. The comparatively poor fit of the negative exponential results from a combination of strong site fidelity and some very long transits. Both of these circumstances violate the assumption of the negative exponential that the probability of a transit ending at any given length is independent of that length.

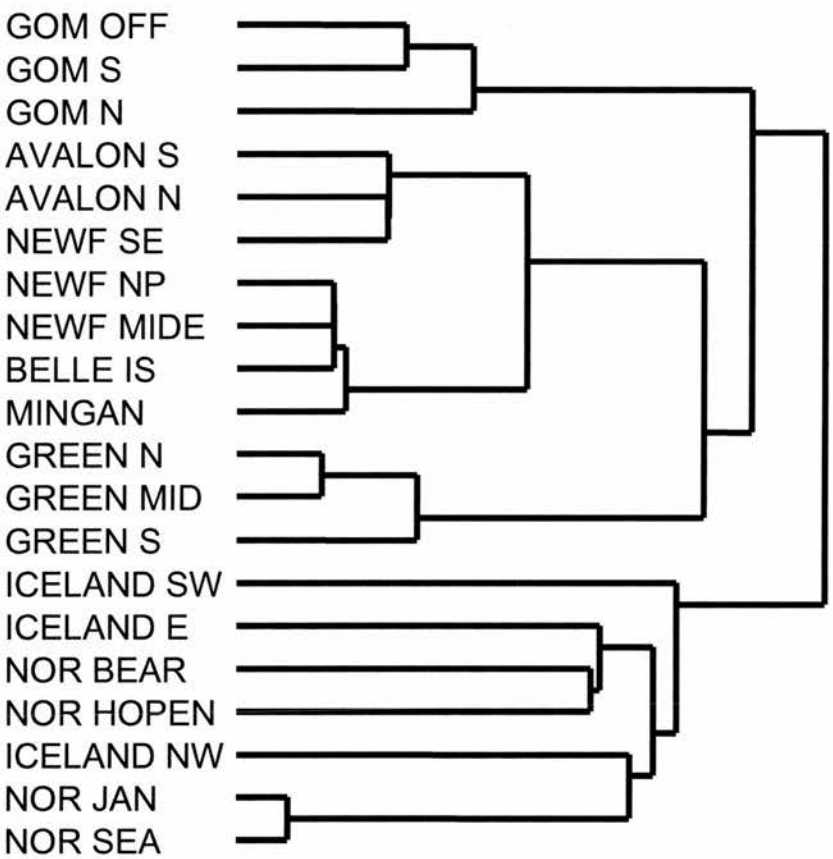

Figure 5.5. Groupings of areas on the feeding grounds within the North Atlantic. The cluster diagram is based upon the standardised deviates for movement between the units illustrated in figure 5.2. The data used are the photographic identifications from 1992 and 1993. Since standardised deviates are not constrained to 0 when there are no re-captures (see Appendix A), the distances at which areas with no re-captures diverge is a function of the sample size.

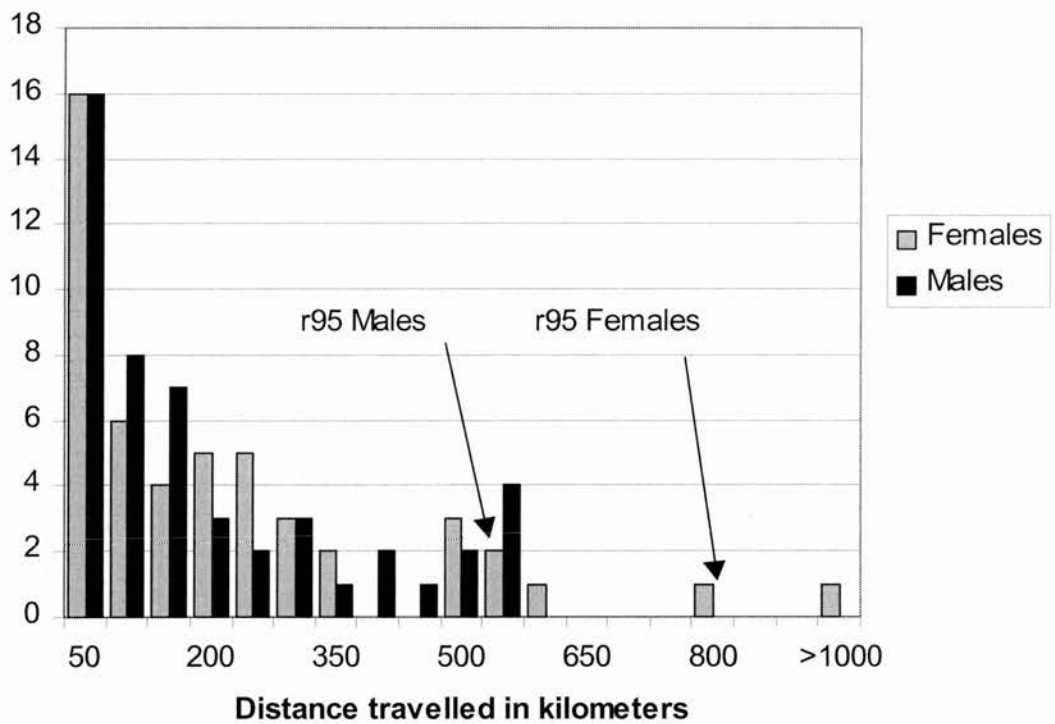

Figure 5.6. Sexual differences in the frequency distribution of between year movement. Animals from the eastern North Atlantic are excluded because of the different overall pattern of movement observed in that region. Arrows mark the approximate radius within which 95% of re-sightings are identified.

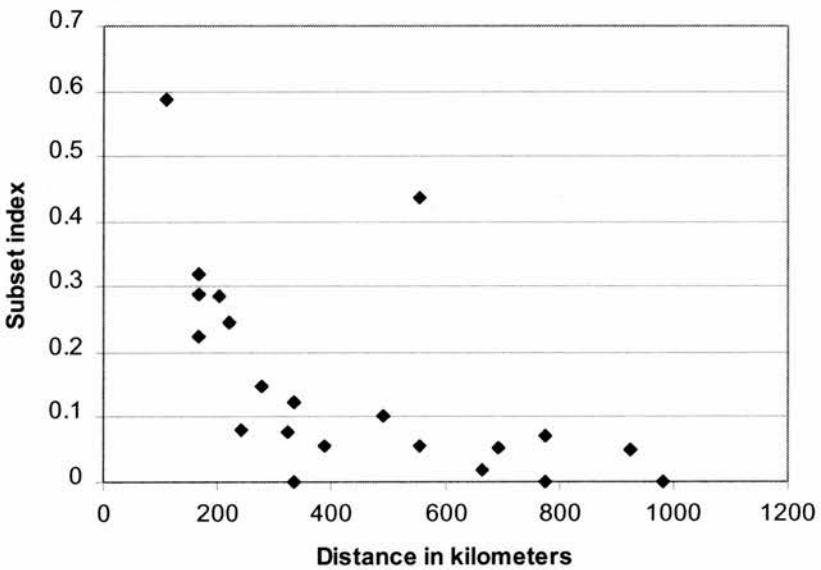

Figure 5.7. Rate of movement between areas illustrated in figure 5.1 and the distance between those areas. The extent of exchange is given as the sub-set index (see Appendix A). The distances are calculated between the location within each area where sampling density is highest. Only movements within the Gulf of Maine, Canada and Greenland are represented because of the different pattern observed in the eastern North Atlantic. Movements between areas within different feeding aggregations are predominantly 0 and are not shown here.

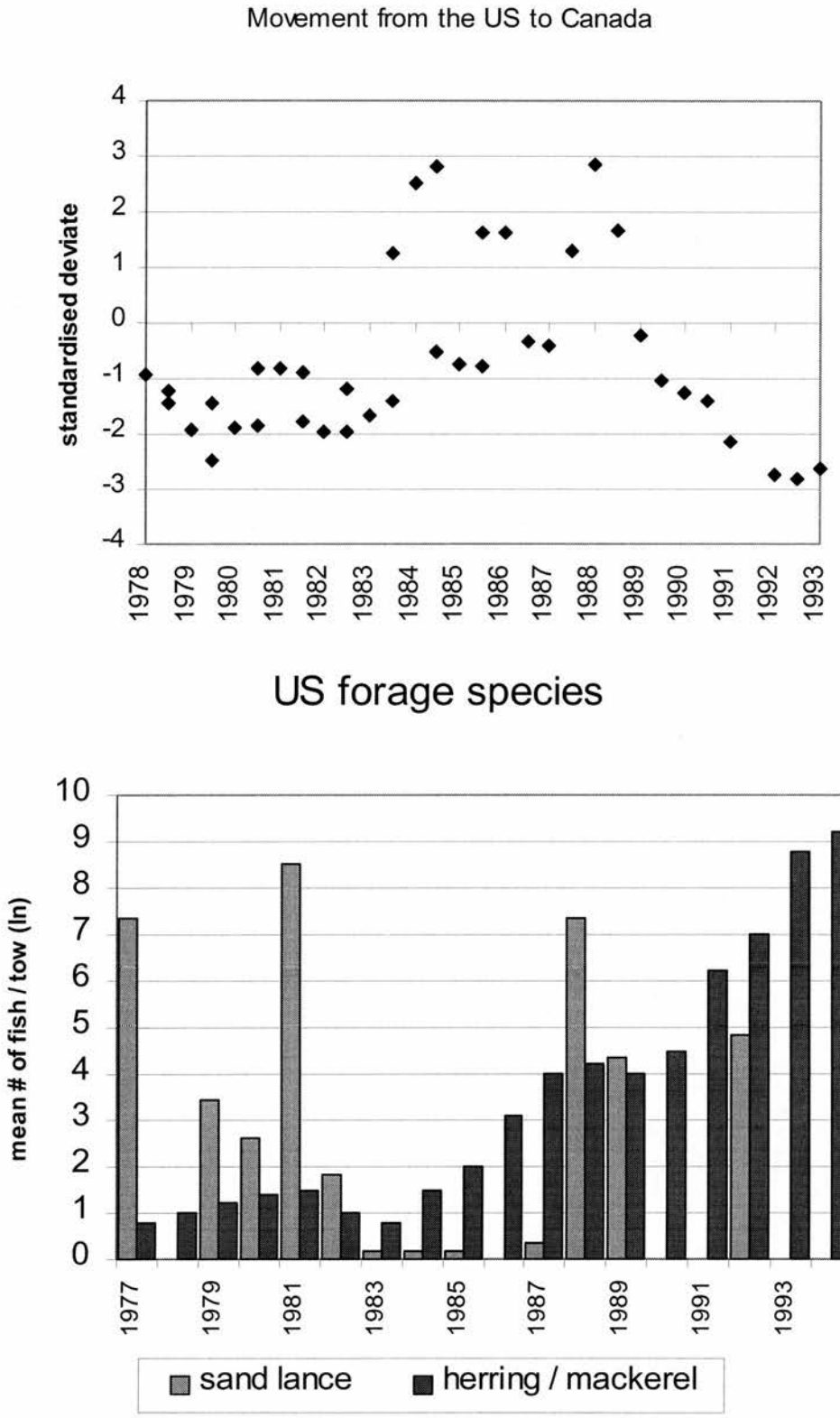

Figure 5.8. Relationship between movement and prey availability. Top- movement of individuals between the Gulf of Maine and Canada represented by the standardised deviates for movement within a year or between two adjacent years. Bottom- two indices of abundance of primary forage species in US waters.

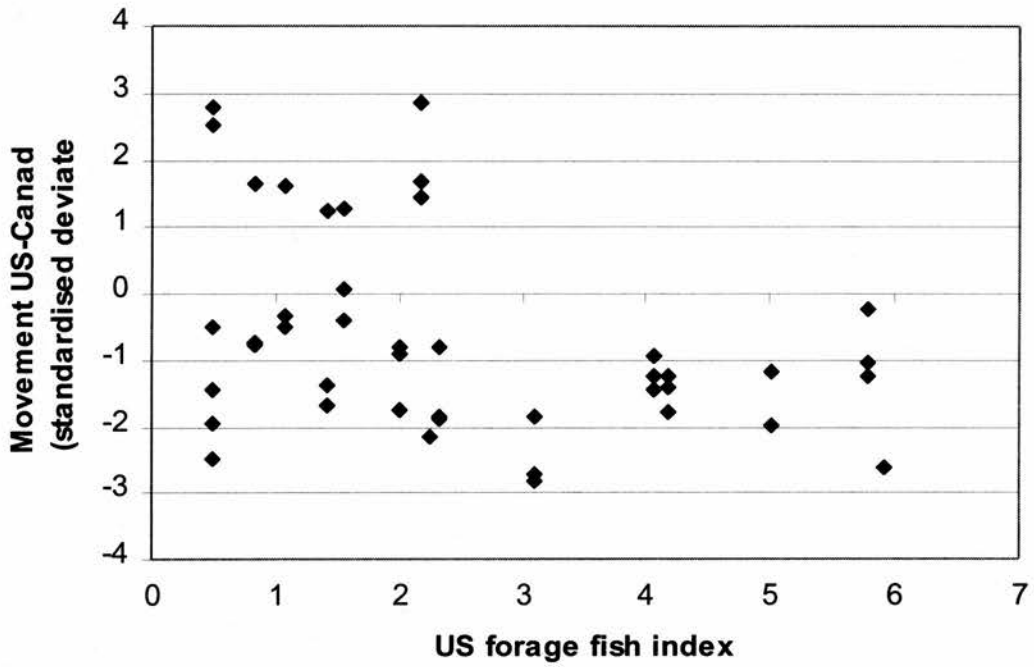

Figure 5.9. The relationship between movement as shown in figure 5.8 and the mean of the two prey indices. There is a onc ycar time lag between the prey and movement indices. Note that there are no positive values for movement rate at fish indices greater than approximately 2.

Chapter 6: Migration timing is related to feeding ground origin in North Atlantic humpback whales: panmixis reconsidered?

Summary

The results of a large-scale, capture-recapture study of humpback whales in the North Atlantic show that migration timing in humpback whales is influenced by their feeding ground origin. No significant differences were observed in the number of individuals from any feeding area that were re-sighted in the common breeding area in the West Indies. A positive but non-linear relationship was demonstrated, however, between sighting date in the West Indies and migratory distance. Mean West Indies sighting dates for individuals from the Gulf of Maine and eastern Canada were significantly different from those for animals from Greenland, Iceland and Norway (9.97 days, t=3.53, df=179, p=0.00054). There is also evidence for sexual segregation in migration; males were seen earlier than females in the breeding grounds (6.63 days, t=1.98, df=105, p=0.050). This pattern is consistent for animals from each feeding area, though the difference is only significant in the western region (8.53 days, t=2.25, df=81, p=0.027). The temporal difference in West Indies occupancy between individuals from the western group and the eastern group coupled with the effects of sexual difference in migratory patterns presents the possibility that there are reduced mating opportunities between individuals from different high latitude areas.

Introduction

Migration is a prominent feature in the lives of most mysticete cetaceans. Many species feed in productive high latitude waters, then migrate thousands of kilometres to low latitudes for calving and in some species also for mating. Even among mysticetes, humpback whales are notable migrants with several instances of 8,000 km migration reported (Darling et al. 1996; Dawbin 1964; Stevick et al. 1999b; Stone et al. 1990). The details of these migrations are poorly known as their often pelagic nature make them difficult to observe. Further, cetacean populations may extend across entire ocean basins, so logistical and resource limitations have restricted most studies to a fraction of this range.

Individual humpback whales show a high degree of fidelity to sites within the feeding range; little exchange is observed between these areas. This leads to structuring of the population evident in movement patterns (Katona & Beard 1990), phenotypic characteristics (Allen et al. 1994) and mitochondrial genetic markers (Palsbøll et al. 1995). However, high latitude origin is thought to have little influence on the breeding system.

Within the North Atlantic, feeding concentrations of humpback whales are found in areas of high productivity extending from the northeast coast of the US to the Barents Sea (Katona & Beard 1990; Smith et al. 1999)(Figure 2.1). Individuals from all North Atlantic feeding aggregations are known to congregate on a common breeding area in the West Indies for mating and calving (Clapham et al. 1993b; Katona & Beard 1990; 1991; Martin et al. 1984b; Stevick et al. 1999b). Current evidence suggests that the existence of a single major breeding ground leads to nearly random mating opportunities relative to feeding

ground origin (Clapham et al. 1993b). However, significant deviation has been reported in the number of individuals from different feeding areas identified in the West Indies (Katona & Beard 1990). Further, non-random association has been shown between animals from some feeding aggregations and specific areas within the West Indies (Katona & Beard 1990; Whitehead & Glass 1985).

There has been considerable uncertainty about the stock structure of humpback whales in the eastern North Atlantic. It has been suggested that eastern and western North Atlantic humpback whales constitute separate stocks, though the specific boundaries of the two stocks and the extent of overlap have been controversial (see reviews by Christensen et al. 1992b; Mitchell & Reeves 1983). Genetic results show some structuring, with differences between samples collected in the eastern and western North Atlantic (Valsecchi et al. 1997). Recent findings that animals from the eastern North Atlantic are sighted later in the West Indies season (Stevick et al. 1999b) suggests that feeding ground origin may influence timing in the West Indies, and therefore mating opportunities.

I use the results of the only large-scale, systematic, capture-recapture study of humpback whales across an ocean-basin to examine migration patterns in North Atlantic humpback whales with respect to timing and feeding ground preference.

Methods

The data presented here were collected as part of the Years of the North Atlantic Humpback Whale project (YoNAH). Sampling for the YoNAH project was conducted during 1992 and 1993 in all of the major feeding areas and the West Indies breeding area (Smith et al. 1999). Standardised sampling protocols

for locating groups of whales, systematically covering groups once located and maximising the chances of successfully sampling each individual were used in all areas as described by Smith *et al.* (1999). Individual animals were identified from photographs of natural markings on the ventral surface of the flukes (Katona et al. 1979). Because the quality of photographs can influence the ability of observers to identify re-sightings, the rate of re-sighting was calculated using only photographs of categories 3+ or better as described by Friday et al (2000). Skin biopsy samples were also collected for genetic analysis. Gender information was primarily obtained from these genetic analyses (Bérubé & Palsbøll 1996a; 1996b; Palsbøll et al. 1992). Where individuals were identified as mothers with calves, but no biopsy samples were collected, these were classified as females. Details of field sampling protocol, survey effort, data collection, and laboratory methods are provided in Chapter 2.

Great-circle distances were calculated using the formula given by Bowditch (1977). Calculated migratory distances did not account for intervening land, as routes travelled are unknown, and in no instances did intervening land require a detour of more than about 300 km from the direct transit. While little is known about arrival or residence times on the breeding grounds, few individuals were seen on multiple days, and the first date on which an individual was identified was used to indicate arrival time.

Individuals were assigned to one of five geographically distinct high latitude feeding areas: the Gulf of Maine, Canada (comprising Newfoundland, Labrador and the Gulf of St Lawrence), west Greenland, Iceland and Norway (Figure 2.1). As there is little information on population identity of individuals from the eastern North Atlantic, data from this region were treated in three

different ways: (i) the pooled results from Iceland and Norway were treated as a single area; (ii) samples from Iceland, the Barents Sea and near Jan Mayen were treated as three separate areas and; (iii) samples collected by the Icelandic and Norwegian field projects were considered as two areas.

In order to compare rates of exchange between the different feeding areas and the West Indies, each feeding area sample was compared with each other sample separately and also with the pooled sample from all other feeding areas. Comparisons were made using chi-square contingency tables or, where expected values were less than five, Fisher's exact tests. In addition to these two-way comparisons between regions, observed re-sightings were compared with the number of re-sightings expected assuming random movement throughout the population, given as:

$$\text{Expected number of re-sightings} = \frac{f_i b}{\hat{N}}.$$

Where:

f_i = sample from feeding area i

b = sample from the breeding area

$\hat{N}$ = estimated abundance

Abundance of humpback whales in the North Atlantic was recently estimated as 11,570 (Chapter 4), and this estimate was used for these calculations.

Migratory patterns

A total of 1508 individual humpback whales was identified in the West Indies breeding area. Of these, 184 were re-sampled at high latitudes during the project of which 58 were identified as males and 49 as females. Migratory distances observed ranged from 2,300 to 8,080 km. Sampling in the West Indies extended from 15 January to 25 March in 1992 and 19 January to 14 March in 1993.

Movement to the West Indies

Individuals from all feeding areas were identified in the West Indies. No significant differences ($p<0.05$) were identified in the number of individuals from any of the feeding areas which were re-sighted in the West Indies (Table 6.1). Nor were the observed movements significantly different than expected, either overall or from any single area (Table 6.2). However, the lowest standardised deviates ((observed-expected)/expected$^{0.5}$; see Appendix A) are to the eastern region representing movement from Iceland, the Barents Sea and the Eastern North Atlantic as a whole. In contrast, the Gulf of Maine, Canada and Greenland have positive standardised deviates. This suggests that eastern animals are under-represented in the West Indies sample to some extent, while western animals are somewhat over-represented, though not at a statistically significant level. The highest standardised deviate is for the Jan Mayen area however, suggesting caution in interpreting these findings.

West Indies sampling was conducted in four areas: Silver Bank, Navidad Bank, Samana Bay, and off the west coast of Puerto Rico. Individuals from the different feeding areas do not appear to be distributed as expected between these

West Indies sampling areas given random mixing (χ^2=26.44, p=0.0093). However, as 13 of 20 cells in the chi-square table had expected values less than five, these results are not reliable.

Timing - east is east and west is west

Overall there was a positive relationship between breeding area sighting date and migratory distance (Figure 6.1). Mean West Indies sighting dates for individuals from the US and Canada (western group) were nearly identical (Feb 16 and 15 respectively), as were those for animals from Greenland, Iceland and Norway (eastern group, Feb 26, 24 and 25 respectively). The mean West Indies sighting date of individuals from the western group was significantly earlier than that from the eastern group (9.97 days, t=3.53, df=179, P=0.00054). Thus western and eastern humpbacks appear to follow different migratory schedules in the North Atlantic, with western individuals arriving significantly earlier.

One potential explanation for the difference in arrival time between these regions is the difference in transit distances to the West Indies. If migratory rates are similar, then individuals with longer transits will arrive later. This, however, would suggest that the relationship between arrival and transit distance should be linear. Alternatively, if food resources are predictably available at different times in the different regions, departure dates may vary as a function of foraging strategy. There are currently few data available with which to evaluate the timing of prey availability and its influence on migration timing.

Sexual segregation in migration timing

Segregation of migration by age, sex or reproductive class has been reported for several baleen whales (Dawbin 1997; Lockyer & Brown 1981; Swartz 1986). In humpback whales such segregation has been noted in migration timing and in the frequency of sightings on the breeding grounds or migration routes (Brown et al. 1995; Dawbin 1997; Palsbøll et al. 1997a). This could further influence the extent to which individuals from different feeding grounds co-occur on the breeding ground.

In this study, males were sighted earlier in the West Indies area than were females (Table 6.3). The effect of sex differences overall is masked by regional timing differences. The significance of the sexual difference is greatest in the western region where sample sizes are larger and regional timing fairly uniform. Males from each feeding area independently were sighted earlier in the West Indies than were females from the same area (Figure 6.2), though none of these differences were significant. Sample sizes from the individual feeding areas are small, as is the sample from the eastern group.

Dawbin (1997) reported on the timing by sex and reproductive status of humpback whales from Southern Hemisphere catch records. Comparisons of catch records with re-sighting records are confounded by the different levels of information available on sex and reproductive class for the two samples, and by different sampling biases. None-the-less, the gender differences in West Indies sighting dates observed in this study do not appear to be consistent with the migratory segregation identified by Dawbin (1997).

No overall difference between adult males and females is evident in the Southern Hemisphere catch data (difference of 0.35 days; Dawbin, 1997). It is known that mothers with newborn calves are severely under-represented in the photographic data as they rarely perform fluking dives. Excluding sightings of females with newborn calves from these results leads to the loss of only four individuals from these data, and changes the mean sighting date for females by only 0.21 days. In contrast, excluding females in late pregnancy from the catch results leads to females migrating on average 5.24 days earlier than males, nearly the reverse of the pattern identified here.

It is possible that individuals in the Northern and Southern Hemispheres have developed different migratory schedules in relation to different selective pressures. Some evidence for inter-area differences in migratory segregation within the Southern Hemisphere is found within the catch data. Several stations, notably Byron Bay, Moreton Island and Norfolk Island show remarkably similar patterns to those identified here, though Dawbin (1997) attributed these to gunner bias.

The effects of segregation

The use of common areas for breeding by whales from different feeding areas, high mobility within these breeding areas, the lack of evidence for preferential association between individuals from common feeding areas and the lack of nuclear genetic structure, have all suggested that mating opportunities in North Atlantic humpback whales are nearly random relative to high latitude origin. The results presented here cast doubt on this conclusion.

These results confirm that individuals from all feeding areas in the North Atlantic visit the West Indies in winter and do so at similar rates. Thus, while some individuals are known to winter elsewhere, (the Cape Verde Islands for example, Hazevoet & Wenzel 2000), these findings support the idea that the West Indies are a primary breeding area for individuals from throughout the North Atlantic.

While differences were observed in the degree to which individuals from different feeding areas were sighted in the different regions within the West Indies, this may or may not reflect preferential associations between these areas, but may be related to the timing of sampling effort in the sub regions. On Navidad Bank, for example, where animals from the Gulf of Maine and Canada are under-represented and those from Iceland and Norway over-represented, only 30% of samples were collected prior to February 19. Similarly, the standardised deviates for the eastern and western feeding groups to the different West Indies areas showed a strong but non-significant relationship with the proportion of sampling early and late season in that region (correlation coefficient=0.612, df=6, ns).

The temporal difference in West Indies occupancy between individuals from the western group and the eastern group, however, presents the possibility that there are reduced breeding opportunities between individuals of different high latitude origins. The mean sighting date for males from the western group is nearly three weeks earlier than that of females from the eastern group (20.41 days, t=3.30, df=50, p=0.0018). Further, it has recently been demonstrated that individual females are located in the West Indies on similar dates in subsequent years, and have a shorter residence time in the breeding grounds (D. Mattila, pers

comm). Thus the geographic origin of the males with which a female mates may be in part a function of her preferred timing in the breeding range.

This reproductive segregation between individuals of different high latitude origin might appear to be at odds with the high degree of genetic uniformity found in humpbacks from the North Atlantic. The segregation shown here is far from absolute, however (Figure 6.1). Only the relative number of individuals from the different high latitude regions varies during the season. Very low rates of gene flow are required to maintain genetic homogeneity, so relative segregation is unlikely to influence the genetic composition of the population.

The sex, reproductive condition and high latitude origin of animals using a breeding area varies during the mating season. While the precise interplay of these factors may be difficult to unravel, they indicate that there is more complexity in the factors influencing mating opportunities in humpback whales than previously assumed.

Acknowledgements

The large data set examined here required the collective effort of many dozens of individuals who supplied assistance in the field, the lab and logistical and financial support. I am greatly indebted to them all. Funding for this analysis was provided by the by the W. E. Anderson trust and by the United States National Marine Fisheries Service under contract #40ENNF800268. This chapter has been prepared for publication with co-authors David Mattila, Jooke Robbins, Judith Allen, Phillip Clapham, Steven Katona, Finn Larsen, Jon Lien, Per Palsbøll, Jóhann Sigurjónsson, Tim Smith, Nils Øien, and Philip Hammond. In particular I am indebted to David and Jooke for allowing me to develop this

material which they arrived at independently though their investigations into the West Indies data. Comments from Ben Wilson, Phil Hammond, Phil Clapham and Jooke Robbins substantially improved the chapter. In addition, many useful comments were received from participants at the Society for Marine Mammalogy conference where some of this material was initially presented.

Regions	Genetic Id		Natural Markings	
	Chi square	P=	Chi square	P=
Gulf of Maine – Canada	0.484	0.487	0.262	0.609
Gulf of Maine – Greenland	0.024	0.877	0.004	0.952
Gulf of Maine – Iceland	0.033	0.856	1.727	0.189
Gulf of Maine – Norway (total)	FE	0.256	0.750	0.387
Gulf of Maine – Norway (JM)	FE	1.000	FE	0.385
Gulf of Maine – Norway (BS)	FE	0.207	3.132	0.077
Gulf of Maine – E. Atlantic	0.640	0.424	2.340	0.126
Gulf of Maine – FG total	0.574	0.449	0.514	0.474
Canada – Greenland	0.101	0.751	0.142	0.706
Canada – Iceland	0.099	0.753	1.241	0.266
Canada – Norway (total)	FE	0.406	0.419	0.518
Canada – Norway (JM)	FE	1.000	FE	0.240
Canada – Norway (BS)	FE	0.346	2.668	0.103
Canada – E. Atlantic	0.102	0.749	1.848	0.174
Canada – FG total	0.136	0.712	0.043	0.837
Greenland – Iceland	0.000	0.988	1.429	0.232
Greenland – Norway (total)	FE	0.311	0.627	0.429
Greenland – Norway (JM)	FE	1.000	FE	0.519
Greenland – Norway (BS)	FE	0.256	2.937	0.087
Greenland – E. Atlantic	0.247	0.619	1.874	0.171
Greenland – FG total	0.061	0.804	0.258	0.611
Iceland – Norway (total)	FE	0.322	0.043	0.837
Iceland – Norway (JM)	FE	1.000	FE	0.154
Iceland – Norway (BS)	FE	0.268	FE	0.521
Iceland – FG total	0.059	0.808	1.481	0.224
Norway (JM) – FG total	FE	1.000	FE	0.228
Norway (BS) – FG total	FE	0.241	2.760	0.097
Norway (total) – FG total	FE	0.301	0.426	0.514
Norway (JM) – Norway (BS)	FE	0.399	FE	0.091
Eastern Atlantic – FG total	0.289	0.591	2.390	0.122

Table 6.1. Comparison of rates of movement to the West Indies between regions in the summer range. Entries listed as FE resulted in expected values of less than 5 and the Fisher Exact test was used to calculate probabilities.

Table 6.2. Deviation from expected number of individuals identified in the West Indies from each of the feeding areas.

Region	Observed	Expected	p=	Standardised Deviate
Gulf of Maine	28	24.1	0.408	0.79
E. Canada	92	88.1	0.657	0.42
W. Greenland	20	17.5	0.534	0.59
Iceland	11	14.7	0.306	-0.97
Norway (total)	7	8.5	0.584	-0.52
Norway (JM)	5	3.0	0.225	1.15
Norway (BS)	2	5.5	0.115	-1.50
E. Atlantic	17	22.8	0.198	-1.22
All regions			0.624	

Table 6.3. Sexual differences in West Indies sighting dates by regions. Sighting dates are given as days of subsequent to the beginning of the year. The eastern region comprises Greenland, Iceland and Norway, while the western region consists of the United States and Canada.

	mean West Indies sighting dates					
Regions	males	females	Difference	t=	df=	p=
All feeding areas	47.45	54.08	6.63	1.98	105	0.050
Eastern region	59.13	63.78	4.64	0.89	22	0.385
Western region	43.37	51.90	8.53	2.25	81	0.027

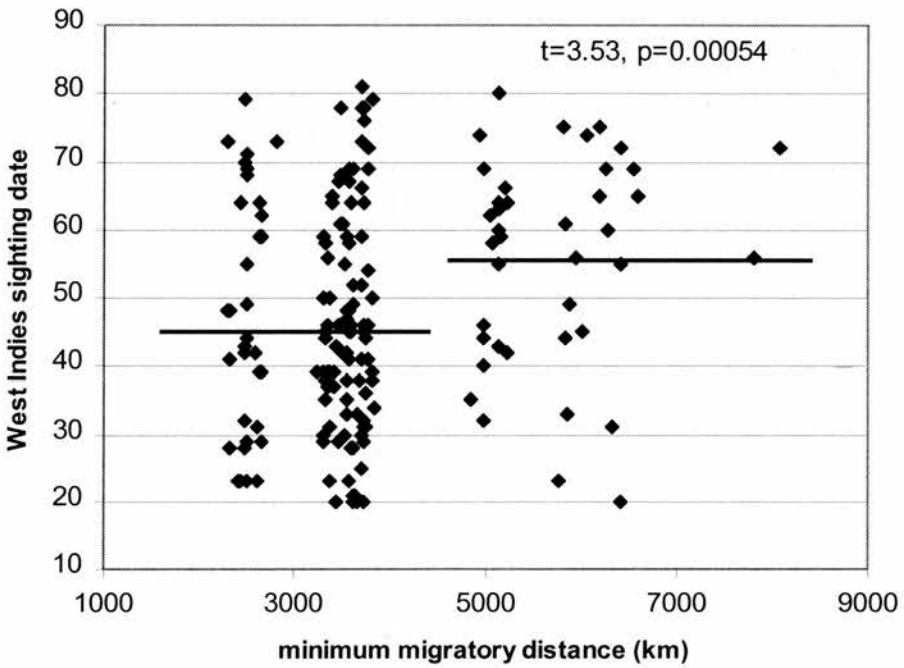

Figure 6.1. The relationship between the minimum migratory transit distance and the first date of sighting in the West Indies. Mean sighting dates for the eastern and western groups are indicated.

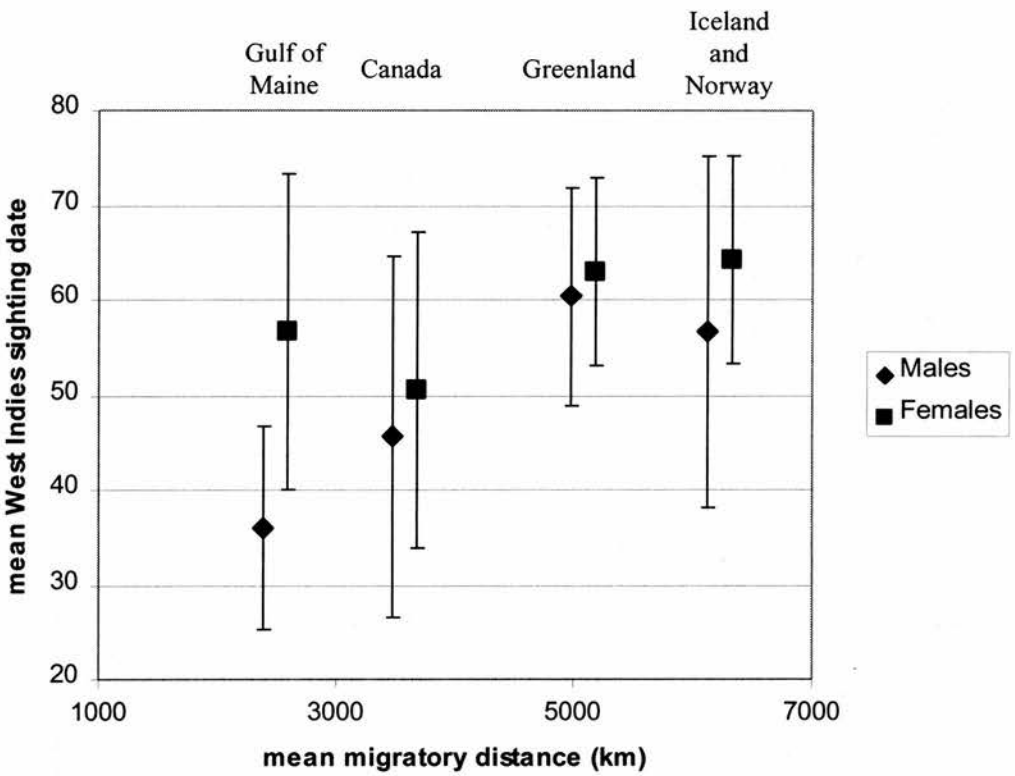

Figure 6.2. Differences in West Indies sighting dates for males and females from the principal feeding grounds (±SE). Iceland and Norway are combined due to the small sample sizes from each area separately.

Chapter 7: Migratory destinations of humpback whales from Norwegian and adjacent waters: evidence for stock identity

Summary

Migratory destinations of humpback whales in the eastern North Atlantic were investigated using naturally marked individuals. A total of 96 individuals was identified from Norwegian and adjacent waters during 1992 and 1993; of these 63 were observed in the Norwegian and Barents Seas, and 33 in the Greenland Sea near Jan Mayen. These were compared with other individuals identified throughout the North Atlantic to identify re-sightings. Ten individuals were identified in both Norway and in the West Indies. There were no significant differences in this rate of exchange to the West Indies between the sample from Norway or either Norwegian sub-area and other feeding areas in the North Atlantic. The mean West Indies sighting date for humpback whales from Norway was 2 March, significantly later than the overall mean for sightings from the West Indies. The individuals identified represent a variety of reproductive classes and both sexes. Observations of mothers with newborn calves, and males in competitive groups provide the strongest evidence to date that the West Indies is utilised as a breeding and calving ground by humpback whales which feed in Norwegian waters. These results suggest that the West Indies is an important, and likely the primary, breeding destination for individual humpback whales feeding off Norway.

Introduction

The migratory destinations of humpback whales from the western North Atlantic have been well documented through photographic identification (Katona & Beard 1991). These data show that while there is considerable site fidelity of humpback whales to specific feeding areas, all or most of the humpback whales from the US, Canada and Greenland congregate on common breeding grounds in the West Indies (Clapham et al. 1993b; Katona & Beard 1990; Katona & Beard 1991)(Chapter 6). While a smaller sample size is available from Iceland, 4 of 20 individuals identified in Iceland were also photographed in the West Indies (Katona & Beard 1991; Martin et al. 1984b). To date, little comparable information has been available to document humpback movements and migratory destinations in the eastern North Atlantic.

An estimated 1,500 humpback whales were taken by Norwegian land stations, mostly off northern Norway between 1881-1904 (Christensen et al. 1992b; Ingebrigtsen 1929). Recently, sighting surveys have shown humpbacks to be seasonally abundant to the north and west of Norway in summer and fall (Christensen et al. 1992b; Øien 1990); however, the stock identity of these individuals is poorly understood. Several authors have suggested the existence of two breeding stocks of humpbacks in the North Atlantic, one along the western and another along the eastern margin of the ocean basin, though the degree of separation and the precise limits of the two proposed stocks have been the subject of considerable disagreement (Mitchell & Reeves 1983).

Catches of humpback whales in winter off the coast of Norway (including takes of females pregnant with large foetuses, Ingebrigtsen 1929) and recent

winter sightings off the Finmark coast (Christensen et al. 1992b) indicate that some individuals may not migrate far from the region. Ingebrigtsen (1929) suggested that humpback whales from Norway travel only short distances for breeding, perhaps to waters off the British Isles. Singing by humpback whales has been reported to the West of the British Isles primarily between October and March (Charif et al. in press; Clark 1995) potentially supporting this idea, though humpback songs have occasionally been reported from other feeding grounds, particularly in autumn (Mattila et al. 1987; McSweeney et al. 1989). The south-westerly progression of these songs from the region of the Faeroe Islands toward the West of Ireland is consistent with them originating from migrating animals, while the track is generally in the direction of the West Indies (Charif et al. in press).

Other authors have proposed that while some humpback whales that summer off of Norway may winter in the Arctic, most move south to breeding grounds in the vicinity of the Cape Verde Islands and along the northwestern coast of Africa (Kellogg 1929; Tomilin 1957; Townsend 1935; Winn et al. 1975). Humpbacks were hunted in winter in these areas (Kellogg 1929; Mitchell & Reeves 1983), and recent sightings from the Cape Verde Islands demonstrate that humpbacks are still found there in winter (Hazevoet & Wenzel 2000; Reiner et al. 1996), though there is little evidence to suggest that large numbers occur in the region today.

Recently, a small number of re-sightings between Norwegian waters and the West Indies have been documented, demonstrating that some humpback whales from Norwegian waters travel to the southwestern North Atlantic presumably for breeding (Palsbøll et al. 1997a; Stevick et al. 1998). In further

analysis of these data presented in Chapter 6, no significant differences were found overall in the rate of movement from different feeding areas to the West Indies, nor were significant differences found in individual comparisons between the rate of travel to the West Indies from Norway and any other feeding ground (Chapter 6). However, the highest negative standardised deviates for movement to the West Indies in this study were to Norway, particularly to the Barent's Sea area (Chapter 6) suggesting perhaps that fewer individuals from this region are re-sighted in the West Indies. While early genetic analyses suggested that the North Atlantic humpback whale population is panmictic, further supporting the theory that all individuals visit the same breeding ground (Larsen et al. 1996), recent studies have demonstrated significant differences in nuclear genetic markers between animals from Iceland and the western North Atlantic (Valsecchi et al. 1997).

Previous results, therefore, leave unresolved the extent to which humpback whales from Norway visit the West Indies in winter and use the area as a breeding and calving site. Sightings of individually identified whales provide one source of evidence for documenting migratory destinations of whales from this region. I report here on the comparison of individually identified humpback whales from Norway with those from the West Indies breeding grounds collected over 14 years, with the aim of assessing the importance of the West Indies as a breeding ground for humpbacks which feed in Norwegian waters.

Methods

Photographs of the ventral surface of humpback whale flukes were collected from the waters off Norway during 1992 and 1993 as part of the Years

of the North Atlantic Humpback Whale project (YoNAH), an ocean basin wide mark-recapture study of humpback whales (Chapter 2, Smith et al. 1999). As part of the YoNAH analysis, these individuals from Norway were compared to the approximately 3,000 other individuals identified throughout the North Atlantic during the YoNAH project to identify re-sightings (Smith et al. 1999). Analysis of migration patterns from the YoNAH data alone are presented elsewhere (Chapter 6, Stevick et al. 1998).

Because of the small sample size from Norway and unresolved questions regarding migratory destinations from this region, all individuals identified by the Norwegian sub-project of YoNAH were subsequently compared to the North Atlantic Humpback Whale Catalog (NAHWC) containing approximately 5,000 identified individuals from the North Atlantic, mostly collected between 1978 and 1991 (Katona & Beard 1990). The results of this comparison are reported here.

Rates of exchange were calculated from Norway to the two West Indies collections separately. A similar rate was calculated from the combined YoNAH feeding ground sub-projects to the YoNAH West Indies for comparison. In 1992 and 1993 YoNAH sampling was conducted in the Norwegian and Barents Seas (Figure 2.1). In 1993, additional sampling was conducted in the Greenland Sea near Jan Mayen, well to the west of the area surveyed in 1992. The distribution of whales identified was discontinuous. Between the two areas of primary concentration there is an intervening distance of 1,200 km in which only a single whale was identified. Because of this discontinuous spatial distribution, exchange rates were calculated separately for the Barents Sea sample and the Jan Mayen sample as well as for the entire sample from the Norwegian project.

Where comparisons between areas resulted in Chi-square cells with expected values less than five, the comparisons were made with Fisher's Exact test.

Because image quality effects re-sighting rates, and image quality varies between collections and areas (Friday et al. in press; Smith et al. 1999), comparisons of re-sighting rates were made based only on good quality photographs of whole flukes. Photographs from the YoNAH collection were restricted to include only photographs coded as categories 3+ and better as described in Smith *et al.* (1999) and Friday *et al.* (2000). Photographs from the NAHWC were restricted to photographs of categories 1 and 2 as described by Katona and Beard (1990).

Dates were converted to sequential days following Jan 1 for computation of means. Photographs of all qualities were used for calculation of sighting dates.

Results

A total of 96 individuals was identified from the Norwegian photographic sample during the YoNAH project. Of these 63 individuals were identified in the Norwegian and Barents Seas (Barents Sea sample), and 33 in the Greenland Sea (Jan Mayen sample). A single whale was identified between the two areas of primary concentration, 620km from the nearest other sighting. Though this sighting was in the Norwegian Sea, it was not allocated to either sub-region because of this ambiguity. The same individual was identified six days later, however, in the Greenland Sea, and that sighting was assigned to the Jan Mayen sample. Of the individuals identified, 85 were represented by photographs which met the image quality criteria for use in calculation of exchange rates, 55 of these from the Barents Sea sample and 30 from the Jan Mayen sample.

Migration to the West Indies

A total of 10 individuals was identified in Norway and also in the West Indies (Table 7.1). Seven of these individuals were identified from the YoNAH collection, while four were identified from the NAHWC, and one in both collections. The pattern of re-sightings differed between the two West Indies collections, with the overall higher re-sighting rate being to the YoNAH collection. Of the Barents Sea sample, two individuals were identified in the YoNAH and three in the NAHWC West Indies collection, while of the Jan Mayen sample, five individuals were identified in the YoNAH and one in the NAHWC West Indies collection. There were no significant differences, however. Re-sighting rates between Norway and the West Indies were not significantly different between collections (χ^2=0.875 p=0.350). Neither were the re-sighting rates different when comparing the returns from the Barents Sea and Jan Mayen samples to the West Indies samples from the NAHWC (Fisher's exact test, p=1.00) or YoNAH (Fisher's exact test, p=0.091). Similarly, there were no differences in exchange with the YoNAH West Indies collection between the total from the feeding grounds in YoNAH and the sample from Norway (χ^2=0.426, p=0.514), the Barents Sea (χ^2=2.760, p=0.106) or Jan Mayen (Fisher's exact test, p=0.228).

No individuals from Norway were re-sighted in the Cape Verde Islands. However, effort in the region has been limited, sea conditions are often difficult, and whales are scattered, so only three individuals have been photographically identified from the Cape Verde region to date. The lack of re-sighting is not surprising, therefore. Subsequent to the data reported here, a larger sample has

been collected from the Cape Verde Islands. No re-sightings have been made to that sample (Hazevoet & Wenzel 2000).

Of the three individuals from which biopsy samples were collected, one was determined to be a male and two female. Four individuals were sighted in competitive groups; one of these individuals on two separate occasions on different banks. The designation of three of these individuals as secondary escorts in competitive groups suggests that these individuals are males, while the other individual was a member of a competitive group where the nuclear animal was identified, so it is also most likely a male, though its role in the group was not specified (Clapham et al. 1992; Tyack & Whitehead 1983). Two mothers with newborn calves were identified.

Transit distances of individuals reported here range from about 6,425km between Jan Mayen and Silver Bank to 8,080km between the Barents Sea and Samana Bay.

Sighting dates in the West Indies

The dates of the West Indies sightings for humpback whales from Norway ranged from 20 January to 25 March. However, there was only one sighting before 19 February. The rest were heavily concentrated in a period of about three weeks in late February and early March, with a mean date of 2 March. In contrast, the mean sighting date for all West Indies whales from the NAHWC was 19 February, while the mean West Indies date for the YoNAH project was 21 February. Thus humpback whales from the Norwegian feeding grounds were re-sighted in the West Indies significantly later than expected from the NAHWC (t=2.79, df=13, p=0.015) and YoNAH (t=2.24, df=13, p=0.043). In

order to minimise the influence of multiple sightings of single individuals within a year, the mean date was re-calculated using only the earliest date for each individual during any single season. While reducing the influence of individual whales on the calculations, this also reduced the already small sample size from Norway, decreasing the power of the test. The mean breeding ground date for individuals from Norway calculated in this manner was 27 February. Using this date, the difference is still significant compared to that for the NAHWC (breeding ground date 17 February, t=2.36, df=10, p=0.040), while the difference with the YoNAH collection is not significant (breeding ground date 20 February, t=1.74, df=10, p=0.11).

The mean West Indies sighting dates for the Barents Sea sample alone are 4 March for all samples and 2 March for earliest sightings only. For the Jan Mayen sample the comparable dates are 28 February and 25 February. The Barents Sea sample is significantly later than the mean for either West Indies collection (NAHWC all sightings t=3.89, df=5, p=0.012; earliest sightings t=3.65, df=4, p=0.022; YoNAH all sightings t=3.30, df=5, p=0.022; earliest sightings t=2.93, df=4, p=0.043). The Jan Mayen sample is later than the West Indies means, but not significantly so (NAHWC all sightings t=1.34, df=7, p=0.22; earliest sightings t=0.99, df=5, p=0.37; YoNAH all sightings t=1.01, df=7, p=0.35; earliest sightings t=0.63, df=5, p=0.55). This temporal segregation is discussed in greater detail in Chapter 6.

Discussion

The results presented here support the finding that humpback whales feeding in the waters off Norway winter in the West Indies (Larsen et al. 1996;

Palsbøll et al. 1997a; Stevick et al. 1998). They further indicate that these individuals represent a variety of reproductive classes and both sexes. The observations of mothers with newborn calves, and of males in competitive groups, provides the strongest evidence to date that the West Indies is utilised as a breeding and calving ground by humpback whales which feed in Norwegian waters. The extent of movement of humpback whales between Norway and the West Indies is similar to that from other feeding grounds. The exchange rate from the Barents Sea to the YoNAH West Indies sample was lower than from other regions, but the difference was not significant, and the trend was reversed in comparisons to the NAHWC.

One reason to suppose that whales from Norway might not travel to the West Indies is the transit distance between the two areas. Humpback whales in Norwegian waters have the most polar distribution of any members of this species, with many individuals occurring north of 70°. While the transit distances reported here are longer than those of most reported humpback whale migrations, these distances are not inconsistent with some documented migratory transits between seasonal habitats in other waters. The distance from Bear Island to the region of the Cape Verde Islands with the highest rate of humpback sightings (Reiner et al. 1996) is 6,890km, only 430km shorter than the distance from the same location to Silver Bank, the major breeding site in the West Indies. At a sustained speed of 6km/hr (Mate et al. 1998) this is a saving of only 3 days on the transit time.

The implications of the later mean West Indies sighting date of whales from Norway are not clear. If, as Ingebrigtsen (1929) and Christensen *et al.* (1992b) suggest, food in the form of capelin is abundant in Norwegian waters in

late autumn and winter, whales may delay departure for the breeding grounds in order to continue feeding. Alternatively, the timing may be a function of distance travelled. The distance from Bear Island to the West Indies is more than twice that from Newfoundland, and nearly three times that from the Gulf of Maine. Thus if all animals depart the feeding grounds at the same time, individuals from Norway might be expected to arrive later. This would imply, however, that either these individuals spend less time in the West Indies than do conspecifics from other areas, or that they remain longer into the spring, arriving on the feeding grounds considerably later than individuals from other areas. There are currently no data to support this. Temporal differences in occupancy in the West Indies would reduce mating opportunities between animals from different feeding areas, though during the middle of the season individuals from all areas are present and substantial segregation seems unlikely. These issues are explored in more detail in Chapter 6.

These findings are consistent with the conclusions of Larsen *et al.* (1996), that North Atlantic humpback whales constitute a single panmictic population. It is likely that some individuals from this region winter outside the West Indies (in the Cape Verde Islands for example, Hazevoet & Wenzel 2000; Reiner et al. 1996), or do not migrate to the tropics at all (Christensen et al. 1992b; Ingebrigtsen 1929). However, these results demonstrate the presence in Norway of individuals which have also been identified on the West Indies breeding grounds in apparently reproductively active roles, and a rate of exchange with the West Indies comparable to that from other feeding areas. This suggests that the West Indies is an important, and likely the primary, breeding destination for the humpback whales from this relatively unstudied feeding stock.

Acknowledgements

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Tables

Table 7.1. Individual humpback whales identified in Norwegian waters and also in the West Indies

ID#s YoNAH (NAHWC)	Date	Location	Latitude Longitude	Gender – Behavior class
Y0081	92/03/12	Silver Bank		Mother – Biopsy Female
	92/09/27	Barents Sea	77°09'N 27°03'E	Biopsy Female
Y0155 (5615)	88/02/25	Samana Bay		Pair
	92/03/09	Silver Bank		In competitive group – Secondary escort
	92/03/25	Navidad Bank	20°04'N 68°50'W	In competitive group – Role unknown
	93/07/21	Jan Mayen	69°30'N 17°36'W	
Y0414	92/03/12	Silver Bank	20°41'N 69°49'W	In competitive group – Secondary escort
	92/06/22	Iceland	65°55'N 27°33'W	
	93/07/21	Jan Mayen	69°30'N 17°36'W	
Y1097	92/07/24	Barents Sea	73°44'N 19°19'E	
	93/02/25	Navidad Bank	20°01'N 68°57'W	In competitive group – Role unknown
Y1132 (5540)	88/03/13	Samana Bay		Mother
	88/03/16	Samana Bay		Mother
	92/07/23	Barents Sea	73°38'N 19°14'E	
	92/09/22	Barents Sea	77°57'N 25°45'E	Biopsy Female
Y1818	93/01/20	Silver Bank	20°46'N 69°51'W	Pair
	93/02/19	Silver Bank	20°45'N 69°47'W	Pair
	93/07/21	Jan Mayen	69°30'N 17°36'W	
Y2067	93/03/06	Puerto Rico	18°22'N 67°17'W	Pair
	93/07/20	Jan Mayen	69°16'N 17°26'W	
Y2250	93/02/24	Silver Bank	20°44'N 69°48'W	Pair – Biopsy Male
	93/07/21	Jan Mayen	69°30'N 17°36'W	Biopsy Male
Y3074	88/02/25	Samana Bay		In competitive group – Secondary escort
(5620)	93/09/05	Barents Sea	76°07'N 25°54'E	
Y3077	83/02/25	Puerto Rico		Singleton
(2307)	93/08/20	Barents Sea	74°21'N 20°49'E	

Appendix A: Methods for quantifying rates of movement between areas using capture-recapture results

Marine mammals typically have a patchy distribution, often demonstrate strong fidelity to habitat units, yet they are highly mobile. Movement between areas, therefore, is variable over a range of temporal and spatial scales (Chapter 5). The extent to which they move between these habitat units determines population spatial structuring, influences the social and reproductive systems and has important implications for management. The degree to which such inter-area movement occurs may be difficult to infer from available data, however.

Capture-recapture methods, based either upon natural or applied marks, are commonplace in studies of marine mammal populations (Chapter 2). These provide an opportunity to investigate movement rates. Estimates of movement rates must account for differences in the abundance of animals and of sample sizes in the areas concerned. As observed rates of movement may be low, indices of movement rates must provide meaningful estimates on the basis of low recapture numbers. Thus data intensive methods are of limited utility in many circumstances.

In this appendix, I consider several approaches of potential use for quantifying rates of inter-area movement in humpback whales using capture-recapture data. I compare the properties and behaviour of three mathematically simple indices that require few data and can be used with only two samples. These are thus applicable to a wide range of situations commonly encountered in

marine mammal studies. I also briefly discuss some more data intensive approaches.

Indices

Sub-set Index

Katona and Beard (1990) presented what they referred to as a sub-set index (*S*) for comparing movements between areas. This is presented as the sum of two proportions:

$$S = \frac{c}{a} + \frac{c}{b}.$$

Where:

a = number of individuals identified in area a

b = number of individuals identified in area b

c = number of individuals identified in both areas.

Note: throughout this discussion sample sizes are not designated as n_i, nor the number of recaptures m_2 as this terminology may be confused with sampling for abundance estimation in which the assumptions about the relationship between samples are very different than they are in this instance. The two should not be treated as equivalent.

The index could also be calculated as the mean of the proportions:

$$S = \left(\frac{c}{a} + \frac{c}{b}\right)/2.$$

Being based upon proportions, the theoretical basis of this method is clear. If presented as the mean, it takes the form of a proportion with values of the index bounded by 0 and 1, while it ranges from 0 to 2 if presented as a sum, though in practice it rarely exceeds half of the theoretical maximum value.

Standardised Deviate

Another way to quantify movement between areas is to compare the observed number of animals identified in both areas to the expected number if movement were random throughout the population (see Baker et al. 1985; 1986; Waite et al. 1999; Whitehead & Glass 1985). The probability of identifying any individual in a (random) sample is the reciprocal of the number of individuals in the population from which the sample is drawn, so:

$$p = \frac{1}{N}.$$

Where:

p = probability of identification

N = abundance.

Since we generally do not know the true abundance we must use an estimate of it. The abundance estimate may be derived in any manner, but the more accurate the estimate of abundance, the more accurate the estimate of capture probability.

If animals mix randomly within the overall area, the product of any two sample sizes and the individual probability of capture yields the number of re-sightings that we would expect to find between those two samples:

$$ab\left(1/\hat{N}\right)=\frac{ab}{\hat{N}}.$$

Therefore, deviations from this expected value indicate deviation from this behaviour pattern, ie. positive deviates indicate higher than expected exchange between samples. The expected value may be used to compare observed and expected values statistically (for example by χ^2). Deviates can also be used as in index of movement. Because absolute deviates are influenced by the magnitude of the expected value, standardised deviates may be calculated as:

$$(\text{observed-expected})/\text{expected}^{0.5}.$$

Rates of movement that approximate random mixing will have standardised deviates near 0. There are no theoretical limits on the range of this index; it can provide large values both positive and negative.

Interchange Index

Two recent studies (Calambokidis et al. 1997; Urbán R et al. 2000) have presented an index of interchange (I) as:

$$I=\frac{c}{ab}.$$

All values are positive, and are generally small. Theoretically the index could reach a value of 1, but only in the unlikely event of both sample sizes being one with a single recapture. In simulations (see below), the value rarely exceeded 0.01. Thus presentation of the index x1000 or x100 depending on observed rates clarifies presentation.

The theoretical basis of this index is obscure as is its origin. In cases where the samples involved meet the assumptions of capture-recapture abundance estimation it comprises the inverse of the Petersen estimator, and therefore the inverse of estimated abundance. This, in turn represents an estimate of the capture probability of an individual (see above). In comparing movement between two areas with limited exchange, however, the assumptions of capture-recapture theory are clearly not met, and the index simply represents the number of re-sightings per comparison of identified individuals. This recapture rate may be influenced by factors other than movement; a high rate of successful comparison may indicate either a small population size or a high rate of movement.

Calambokidis, et al. (1997) and Urbán R, et al. (2000) cite the index as being developed and used by Baker et al. (1985; 1986), though it is not used in either of these papers. The estimation of capture probability is presented there, however, where it is used to calculate expected values for chi-square comparisons of movements between areas in the same manner as outlined above. The terminology and formula used by Baker et al. (1985) to present capture probability of an individual are nearly identical to those used to describe the Interchange Index (Calambokidis et al. 1997; Urbán R et al. 2000). This suggests

that the Interchange Index may derive from a mis-interpretation of the use capture probability by Baker et al (1985).

Comparison

In order to compare the behaviour of the three indices, they were applied in simulations to data generated from a simple model. This was constructed in two stages. Initially two areas were designated. The numbers of individuals using each area were selected randomly from a uniform distribution, and ranged from 30 to 500. The number of individuals occurring in both areas was calculated as the product of the mean sample size and a randomly selected transition probability, also selected from a uniform distribution. Instances where the predicted number in common to the two areas exceeded the smaller regional abundance, were not used in this analysis. From each of these simulated areas a sample of between 20 animals and the total abundance of the area was selected randomly, and the recaptures between the two samples were identified.

The three indices were calculated for each replicate. The Sub-set Index was calculated as the mean, the Interchange Index was calculated x100 and the Standardised Deviate assuming an overall abundance of 3,000. These indices were compared with the transition probability from the simulation to see how well they represented the underlying movement processes.

The results from 1,000 replicates of the simulation are presented in Figure A1. All three models show a strong positive relationship between the index value and the transition probability ($p<10^{-9}$ for all 3 indices). In order to compare performance, correlation coefficients were computed and analyses of variance were conducted for each index (Table A1). The Standardised Deviate performed

most successfully, while the Interchange Index performed least well. The pattern of results from the Sub-set Index and the Standardised Deviates were remarkably consistent, though there was slightly less variability in the Standardised Deviates as is apparent from the F-ratio and r^2. There was a weaker relationship between transition probability and the Interchange Index by both measures. There were a larger number of estimates well above the overall trend; in linear regression, 14 of 1,000 estimates were identified as outliers (studentised residuals > 4), while only one outlier was identified in the Sub-set Index and none among the Standardised Deviates.

Sample size had a substantial effect of the performance of all indices. Cases with one or no recaptures occurred across the range of transition probability values leading to low values of all indices. At low transition probabilities these reflected few animals actually occurring in both areas and null values might occur at a range of sampling intensities (sample size/group size). In this circumstance index values reflecting a lack of recaptures are an appropriate indicator of movement rates. At high transition probabilities, however, they are an artefact of low sampling intensity. The highest values at any transition probability also occurred with small samples, particularly when coupled with high sampling intensity. In this situation the number of recaptures occasionally approached the lesser sample size.

Recommendations

All three indices performed well, but by no means equally well.

The Standardised Deviate performed best of the three methods over a range of sample sizes and sampling intensities and has several advantages over

the other methods considered. Unlike the other indices it compares observed movement against expectation based upon assumptions about abundance and individual behaviour. This comparison of observation and expectation lends itself to statistical comparison in a manner which the other approaches do not. Further, this technique allows for quantification in cases where no recaptures at all are observed, while the other indices are constrained to 0 in this situation.

The major disadvantage of this method is that it is dependent on an estimate of abundance, and this is often not available, or may be highly biased, while in a geographically stratified population it may not be clear what regions should be included in the abundance estimate to be used. Fortunately, while variations in the abundance estimates used will influence the absolute value of the Standardised Deviate, relative values are not sensitive to the value of N.

The Sub-set Index performs nearly as well as the Standardised Deviate over a range of circumstances, though it produces slightly more variable results. Both Standardised Deviates and the Sub-set Index are used for analysis in this thesis.

Due to the relatively poor performance of the Interchange Index compared with the other indices, the frequency with which it produces anomalously large values, and questions concerning its mathematical and theoretical basis, the use of this index would not appear to be advisable and it is not used in this thesis.

Maximum likelihood estimators

A number of maximum likelihood estimators have been developed which provide estimates of parameters useful in assessing movement rates. While these

require substantially more data, are sensitive to violations of model assumptions and are, therefore, less widely applicable, I will discuss some of them briefly here.

Estimators have been developed for abundance of geographically stratified, closed populations. Most of these are based upon the two-sample estimator proposed by Darroch (1961). The Darroch model estimates transition probability between strata directly as one of the model parameters, and thus can be used to quantify movement between areas.

One limitation of this method, as recognised by Darroch (1961) is that it may produce unrealistic parameter values (capture probabilities >1 for example). This is due to the complexity of computing multiple parameters from limited data, and the problem can only be remedied, therefore, by high sampling intensity and large sample sizes (Dorazio & Rago 1991). Another limitation is that the technique cannot be used where singularities exist in the matrix of recaptures between strata. This may be particularly problematic where there are numerous strata between which no exchange is observed (Schwartz & Taylor 1998). Pooling strata has been used as a means of minimising these problems, resolving both singularities and cases that fall out of range (Arnason et al. 1996; Darroch 1961; Schwartz & Taylor 1998).

I conducted simulations of the Darroch model in conjunction with Dr. J. Matthiopoulos. These were based on a hypothetical population of 1000 individuals occurring in 4 strata. Simulations covered the full range of strata abundances and transition probabilities. Replicates that produced singularities were excluded.

These simulations demonstrated that estimates of unreasonable parameter values occurred across the full parameter space, accounting for about 10% of the replicates which did not produce singularities. They further demonstrated that substantial biases in parameter estimates occurred even when estimates fell within theoretical bounds. For replicates with estimates falling within theoretical limits, approximately 43% had estimated values for the transition probability with biases greater than 10%, while about 5% had biases of more than 50%. This was also true across the parameter space. Thus, these simulations raise doubts about the reliability of estimates derived in this manner, even when they appear reasonable, and the approach of pooling strata to produce acceptable estimates would also appear to be suspect. The exception to this would occur if sampling intensity were very high (Dorazio & Rago 1991), though it is unclear how great sampling intensity would have to be, or how results could be tested to confirm their reliability. Because of these uncertainties about the behaviour of stratified estimators even if all assumptions of the model are met and the parameter values appear reasonable, the method is not used in this thesis.

Multiple re-capture models

Transition probabilities have also been estimated directly using multiple-recapture open-population models (see Hestbeck et al. 1991). In an alternative multiple-recapture approach, Whitehead (1990) developed a temporary emigration model which calculates rates of emigration and re-immigration. This technique has recently been applied to quantify movement patterns of dolphins (Durban et al. 2000). This method examines rates of movement into and out of sampled areas rather than specifically movement between pairs of areas.

Multiple recapture models are data intensive, requiring large sample sizes over several sampling intervals, and are relatively sensitive to heterogeneity of capture probabilities (Pollock et al. 1990; Seber 1982). Large, representative samples from two or more locations simultaneously over numerous sampling intervals are rarely available in marine mammal studies. Because of limitations in the data available on North Atlantic humpback whales, I have not used multiple recapture methods for any analyses in this thesis.

Acknowledgements

Astute questions from Finn Larsen prompted me to compare these indices in a more methodical manner and, therefore, brought this appendix into being. Jason Matthiopoulos brought considerable programming expertise and a healthy dose of scepticism to the analysis of stratified estimators. Catriona Stephenson provided advice on programming for the simulation of movement indices.

Tables and Figures

Table A.1. Analyses of variance for three movement indices based on 1,016 replicates of the simulation model.

Index	Mean-Square regression : residual	F-ratio	r^2	p
Standardised Deviates	22,015 : 10.81	2,037	0.668	***
Sub-set Index	34.76 : 0.018	1,921	0.655	***
Interchange Index	793.88 : 1.48	538	0.347	***

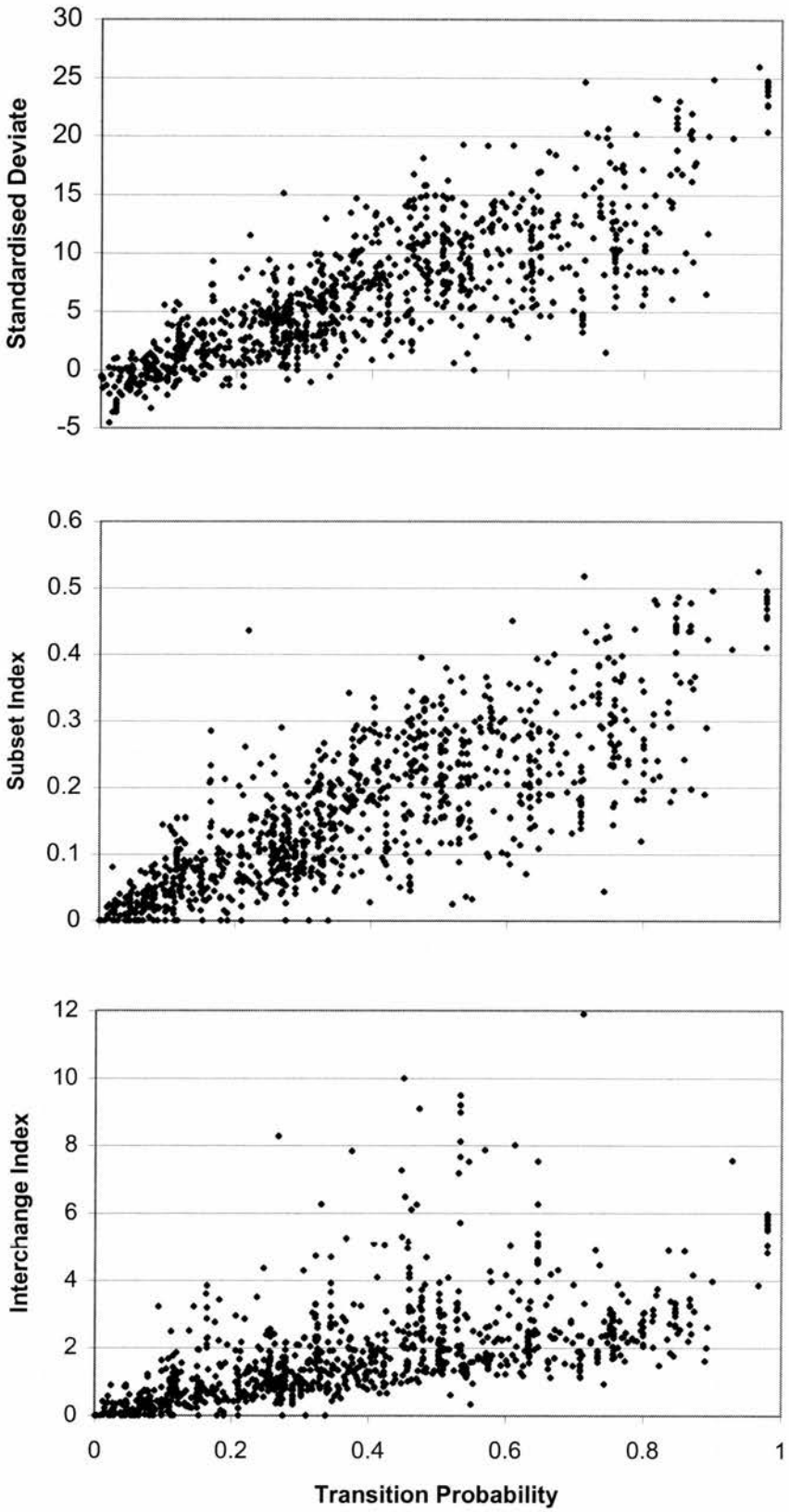

Figure A.1. The relationship between three movement indices and the transition probability between areas. Data are from 1000 replicates of a simple simulation model described in the text.

Appendix B: Variance estimates and confidence intervals for abundance estimates using the correction for identification errors

Variances for the error corrected abundance estimator presented in Chapter 5 were estimated by a parametric bootstrap procedure. This procedure was principally designed by Mark V Bravington (CEFAS, Lowestoft Laboratory, Suffolk, UK). This appendix presents his description of the method with only minor editorial input from me.

Estimates of variance and confidence limits for N can be obtained by bootstrapping where the appropriate resampling unit is the individual whale. The obvious nonparametric bootstrap cannot be used because we cannot be sure of the identity of every whale. However, it is possible to devise a parametric bootstrap that retains some useful robustness. Although the estimation framework assumes that there is negligible heterogeneity of capture probability *between* samples, there is still the possibility of *within* sample heterogeneity, whereby some whales get photographed significantly more than others within a given year. This is likely to result from, for example, different whales having different patterns of habitat use, and thus different exposure to photo opportunities. To obtain reliable inferences, we must ensure that any such within-year heterogeneity is mimicked in the bootstrap re-samples. Because uncertainty in identification must be taken into account, it is most practical to investigate heterogeneity using only quality-1 photographs (for which identification of the

whale is assumed certain), and then to extend the results to photographs of all qualities.

In any given season, suppose that the i^{th} whale has an "intrinsic photographability" of λ_i, defined as the expected number of quality-1 photographs of the whale. The value of λ might vary among whales, depending on their behaviour; however, within-season variations in each λ_i are not important because the role of λ is to parameterise the total number of quality-1 photographs across the whole season. Assuming that photographs of the same whale are independent conditional on its λ, then the distribution of M_{i1}, the actual number of quality-1 photographs of the i^{th} whale in the whole season, is Poisson with mean λ_i, so that

$$\{\mathrm{P} \mid M_{i1} = m\} = \frac{e^{-\lambda}\lambda^m}{m!}.$$

The probability that a randomly chosen whale will be photographed m times is thus

$$p_m = N^{-1}\sum_i \frac{e^{-\lambda_i}\lambda_i^m}{m!}.$$

For large N, we can approximate the population distribution of λ by a continuous distribution with density $f_\lambda(.)$, so that for a randomly chosen whale

$$p_m \approx (m!)^{-1}\int e^{-\lambda}\lambda^m f_\lambda(\lambda)d\lambda.$$

The total number N_m of whales with m quality-1 photographs in the season is Binomially distributed with limit N and probability p_m. Since N is large, this is well approximated by a Poisson distribution with mean Np_m.

Note that one might equally well explain the data by assuming (i) that whales all have the same photo probabilities, but (ii) that being photographed on day X increases the probability of the same whale being photographed on (subsequent) day Y. Fortunately, the distinction is metaphysical from the viewpoint of mimicking the data, precisely because the data can be explained equally well either way. For the sake of tractability, we adopt the independence scheme above.

If all photo probabilities are the same (i.e. the distribution of λ is concentrated at a single point), then the distribution of m across all whales will also be Poisson. This can be studied by a χ^2 test. Appendix1, Table 1 shows that the equal-probability hypothesis is tenable for the breeding-ground data set (where there is no whale that has more than one quality-1 photo, which is a good fit to a Poisson distribution) but not for the feeding-ground data (χ^2 statistic on groups 0, 1, 2+ is 87.47, 1 df: $p < 0.0001$), so that estimation of heterogeneity is required. If we were only interested in quality-1 photos, all that would be necessary would be to resample from the empirical distribution of m. However, since we need to simulate all qualities of photo, it is necessary to estimate something about the underlying distribution of λ. Clearly, we only have a small number of informative observations (number of whales with 0 quality-1 photos, number of whales with 1 quality-1 photo, etc.) so we cannot expect to recover a full continuous distribution for λ. Again, this is fortunately a metaphysical problem; all we need is an approximate distribution for λ that mimics the data. An efficient way to do this is to assume that λ follows a discrete distribution with support at R pre-specified points $\pi_1 \ldots \pi_R$, and corresponding weights $w_1 \ldots w_R$ to

be estimated, subject to the constraints $w_r \geq 0$, $\Sigma w_r = 1$. Details are given below in the section on estimating heterogeneity.

Once we have estimated the extent of heterogeneity for quality-1 photos, it is easy to work out the distribution of all qualities of photographs, assuming photo quality is independent of the number of times a whale is photographed. Suppose the i^{th} whale has intrinsic photographability λ at quality-1. The distribution of number of quality-1 photos of that whale is Poisson with mean λ, and the distribution of number of photographs of *any* quality for that whale is simply Poisson with mean λ/q_1, where $q_1 = \text{P}\{\text{quality of photo} = 1\}$. This leads to a conceptually simple parametric resampling scheme, as follows.

1. For the i^{th} whale in the population, randomly pick its quality-1 photo rate π^{i*} from the set π according to the probabilities w.
2. Pick m^{i*} the total number of photos of that whale, from the Poisson distribution with mean π^{i*}/q_1.
3. Allocate the m^{i*} photos to quality category according to a multinomial distribution with probabilities $q_1, q_2, \ldots$.
4. For each photo that is not of quality-1, decide whether it is correctly identified to the i^{th} whale, using a Bernoulli distribution.

Although this procedure is simple, repeating it for all $\hat{N}$ whales is very slow. It is much more efficient to start by deciding how many whales get photographed 0, 1, 2, ..., times, by sampling from a multinomial distribution with limit $\hat{N}$ and $\text{P}[m] = \sum_r w_r \exp\{-\pi_r / q_1\}(\pi_r / q_1)^m / m!$. The whales which are

not photographed at all (the vast majority) can then be ignored, and steps 3 - 4 above can be applied to each of the remaining whales.

Estimating heterogeneity

Given a fixed set $\pi = \{\pi_r, \ldots, \pi_R\}$ which constitutes the support of a discrete distribution for λ the problem is to maximise the log-likelihood of the data over the weights $w = \{w_1 \ldots w_R\}$ subject to $w_r \geq 0$, $\Sigma w_r = 1$. It is most convenient to re-parametrise as $\nu_r = Nw_r$ without the second constraint, so that the log-likelihood is given by:

$$\Lambda(w;n) = \sum_m \{-Np_m + n_m \log(Np_m) - \log(n_m!)\}$$

$$= \sum_m \left\{ -\sum_r \nu_r q_{mr} + n_m \log\left(\sum_r \nu_r q_{mr} \right) \right\} + const$$

where

$$p_m = \frac{1}{m!} \sum_r w_r e^{-\pi_r} \pi_r^m = \sum_r w_r q_{mr}$$

$$Np_m = \sum_r \nu_r q_r$$

This can be maximised over ν by iterative quadratic programming, as follows:

1. At each iteration, given the current trial value $\nu^{(i)}$, calculate $g^{(i)} = d\Lambda/d\nu$ and $H^{(i)} = d^2\Lambda/d\nu^2$.

2. Identify the appropriate active set $\Re = \{r : \nu_r^{i+1} \geq 0\}$ for maximising the approximation $\tilde{\Lambda} = (\nu^{(1+1)} - \nu^{(i)}) g^{(i)} + (\nu^{(i+1)} - \nu^{(i)})^T H^{(i)} (\nu^{(i+1)} - \nu^{(i)})$ over $\delta\nu$.

This is done by initialising $\Re = \{1 \ldots R\}$ and then iteratively removing any r for which $\nu_r^{(i)} = 0$ and where, in the absence of constraints, $\widetilde{\Lambda}$ would be maximised by decreasing ν_r while keeping $\nu_s \equiv 0 \ \forall \ s \in \Re$.

3. Find an approximate maximum for the full likelihood Λ along the direction of maximum improvement for $\widetilde{\Lambda}$ over the set $\nu_{\Re}$. This amounts to first trying the full Newton-Raphson step for $\widetilde{\Lambda}$, and taking smaller steps in the same direction if Λ itself is not increased. The positive-semi-definite character of $H^{(i)}$ ensures that this is always possible for a small enough step.

Some experimentation is required to choose an appropriate π. Because of the smearing and grouping of the λ-distribution induced by the Poisson compounding, fine details of the λ-distribution have no impact on the final distribution of number of photographs. The fitting procedure seems numerically stable in practice as long as R is not larger than the maximum number of quality-1 photographs of any whale. While this might sound like over-parameterisation, it is important to remember that the goal is not to estimate the underlying λ-distribution (for which there is no unique solution), but rather to provide a probabilistic data-generating mechanism that matches the empirical data. This is in line with the spirit of bootstrapping, where the basic idea is to resample from the full empirical distribution of the data.

Tables

Table B.1. Number of whales with different numbers of quality-1 photographs from the summer 1992 and winter 1992 data sets. Abundance is 12,693 (standard Petersen estimate). For FEEDING 1992 the maximum number of sightings represented by quality-1 photographs per whale was 3. For BREEDING 1992 the maximum number of sightings represented by quality-1 photographs per whale was 1.

Number of whales with 0-3 quality-1 photos		0	1	2	3
Data set: FEEDING 1992.	Observed	12,447	228	14	4
	Expected	12,428	262	2.8	0.02
Data set: BREEDING 1992.	Observed	12,558	135	0	0
	Expected	12,559	134	0.7	0

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